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SYMMETRIES AND THE ROLE OF THE MANTLE MARGINS IN THE BIVALVE MOLLUSCA

C.M. Yonge

ABSTRACT

Evolution throughout the Mollusca is explicable as the consequence of diverse interactions between the bilaterally symmetrical viscero-pedal mass and the radially symmetrical mantle/shell, which gives protection and overlaps the respiratory ctenidia. Following lateral compression, the Bivalvia become enclosed within calcified valves and a mid-dorsal, uncalcified ligament. Further evolution is controlled by the mantle/shell by way of the middle and inner marginal folds. The middle marginal folds usually carry receptors, and in some bivalves the middle folds emerge to assist – even replace – the valves in penetration of calcareous rock. In other bivalves, the middle folds completely enclose the valves. The inner folds control water flow, their radial muscles atttached along the pallial line, cross fusing at both ends forming adductors, pallial like the ligament they work against. Fusion of mantle margins in the Mesozoic produced increasingly complex siphons, giving wider range of habit. Fusion of periostracal grooves (or of their secretions) extended the primary ligament, leading to formation of a secondary, more dorsal ligament. Control of form and habit also is shown by the effects of a tangential growth component in the Chamacea and in *Cleidothaerus* (Pandoracea) and by those of cementation in the Etheriidae (Unionacea).

Descending possibly from turbellarian-like ancestors, the first molluscs basically consisted of ventral foot and dorsal mantle with intervening viscera (Stasek, 1972). Paired ctenidia with central axis and lateral filaments bearing cilia for current production and for cleansing appeared laterally beneath an overhanging mantle that secreted an initially non-calcareous shell. Variously modified (multiplied, reduced or hypertrophied), these structures continue to meet the respiratory needs of all marine molluscs apart from the Scaphopoda and the opisthobranchiate Gastropoda but including the Cephalopoda (Yonge, 1947). In the Bivalvia, the single pair of ctenidia enlarge to form elaborate, highly efficient ciliary feeding mechanisms.

Thus, bilaterally symmetrical animals with laterally projecting gills and associated organs came under the protection of a radially symmetrical mantle/shell, the two united by paired pedal, or shell, muscles. Evolution in the Mollusca is explicable only as the outcome of the diverse interactions between these symmetries. Its understanding, therefore, demands acquaintance with the separately originating, and still frequently independently studied, subject matters of malacology and conchology.

Retention of the primitive crawling habit, the elongate mantle secreting an articulating shell with multiplied ctenidia occupying narrow pallial grooves (Yonge, 1939a), produced the Amphineura adapted for life on irregular hard surfaces. Dorsal extension with resultant coiling led, if followed by torsion, to the epifaunal and secondarily infaunal or pelagic Gastropoda; if followed by separation of apical, gas-filled chambers, they led to the pelagic Cephalopoda. In the former, with anterior mantle cavity, apotheosis is attained in neogastropods, where prey is detected in the respiratory current entering through an exploratory pallial siphon and tested by a probably originally sediment-detecting osphradium (Yonge, 1947). In the predatory decapod Cephalopoda with internal shell, the mantle cavity (still the respiratory chamber, although with reversed, muscle-created current passing between complexly folded ctenidial filaments; Yonge, 1947) becomes the means of jet propulsion.

In the Amphineura, form and habit are dominated by the mantle; in the Gastropoda,

conditions range from complete mantle domination, as in the cemented, worm-like vermetids, to loss of the mantle/shell and reversion to almost complete bilateral symmetry in the nudibranchs. In the Cephalopoda, symmetries blend; mantle cavity and head both face anteriorly, while the ventral foot becomes a mobile funnel directing the jet stream.

In the Bivalvia, the animal becomes enclosed within its respiratory cavity, the visceropedal mass profoundly and irrevocably affected. The head is lost, while the compressed, terminably distended foot with paired retractors pulls the animal through the soft substrates it now inhabits (Trueman, 1968). The bivalve form is here considered to have evolved *prior* to calcification (Yonge, 1953a), the mantle consisting of lateral lobes with a uniting mid-dorsal isthmus (Owen et al., 1953). The lobes secrete the valves, the isthmus the inner layer of the *primary ligament*. The outer layers of both, as noted below, are formed by the outer marginal folds.

Beneath the mantle isthmus, the mantle lobes unite to form the pallial crest which, creating teeth on one side and sockets on the other, produces the hinge plate with its characteristic dentition (Fig. 5C). The hinge, therefore, consists of a ligament producing the opening moment (Trueman 1964) and the teeth which ensure valve alignment after adduction. In the boring Adesmacea, this no longer applies, the separated valves rock on the dorso-ventral axis. Form in the Bivalvia is dominated by the mantle/shell, the valves adapted as a means of rock or wood boring in some or all members of six superfamilies and also of swimming in some Pectinidae and Limidae.

The early Cambrian Rostronchia are claimed as ancestral to the Bivalvia (Runnegar, 1978), but the compressed, presumably infaunal, shell lacks ligament and adductors and so could neither open nor close. The Rostroconchidae appear to have calcified prematurely to be ousted by the possibly related but better adapted Bivalvia where calcification followed complete lateral compression.

Pallial enclosure involved withdrawal of the mouth and loss of cephalic sense organs. Food presumably initially consisted of organic detritus collected by protruding lip appendages, as in the modern protobranch Nuculacea, with later evolution in the Nuculanacea of pumping ctenidia (Yonge, 1939b) and extensive exploitation of the abyssal environment (Allen, 1979). The lamellibranch ctenidium ensured increased water flow with highly efficient filtration of suspended material, especially phytoplankton. Accompanying sediment – always a problem in gill chambers – together with particles rejected by the now solely sorting labial palps, was collected in the ciliary rejection tracts (first fully described by Kellogg, 1915). These aptly designated pseudofaeces (Dodgson, 1928) were rejected from the inhalant chamber, sometimes, as in the Tellinacea, finally through overhung channels, by sudden contractions of the striated "quick" muscle, which came to occupy distal areas in both adductors.

Sensory contact with the environment had to be re-established and control imposed on the greatly increased water flow. Development of additional folds around the mantle margins solved both problems and also was to be the means of acquiring new habits and exploiting fresh environments. Their potential was responsible for the striking success, despite enclosure within the mantle/shell, of the Bivalvia.

Throughout this class, with the recently established exception of some Arcoida (see below), the mantle is fringed by three folds (Fig. 1). The outermost is a basic molluscan structure (Stasek & McWilliams, 1973) forming the outer shell layers. It is bounded internally by a groove from which emerges the non-calcareous periostracum, which initially covers the entire surface of the shell. Within the pallial space below this, the outer surface of this fold secretes the outer (prismatic or crossed-lamellar) layer of the valves (Taylor et al., 1969) and, at each end of the mantle isthmus, the anterior and posterior outer (lamellar) ligament layers (Yonge, 1978a).

Although additional folds appear in other molluscs, the middle and inner folds in the Bivalvia meet the particular needs imposed by compression and enclosure. With distal surfaces covered by periostracum, the middle folds, first in contact with the environment, assume

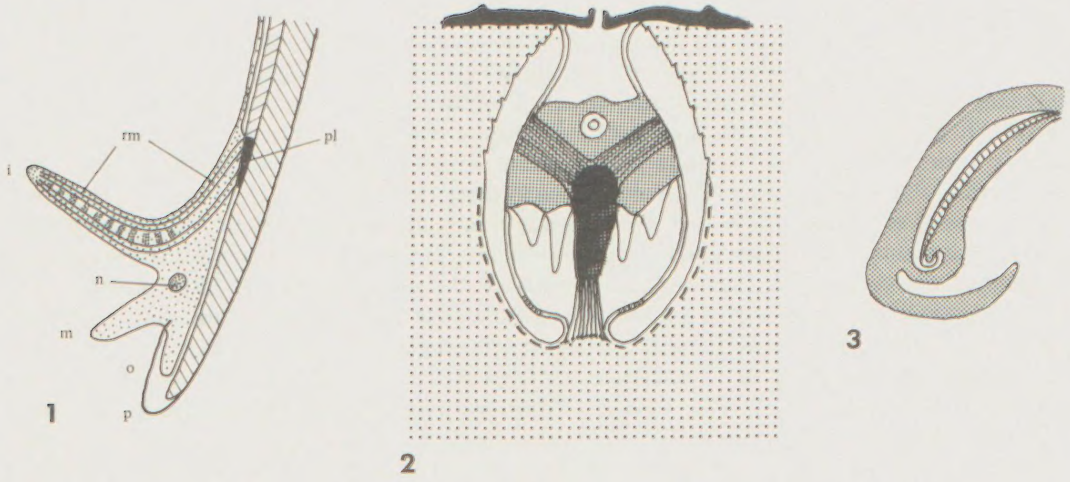

FIG. 1. Formal transverse section through margin of mantle lobe and valve of typical bivalve, outer fold (o) secreting outer calcareous layer of valve with superficial periostracum (p) issuing from groove at base, middle (sensory) fold (m) with nerve (n), inner fold (i) with radial muscles (rm) attached to valve along pallial line (pl). FIG. 2. *Tridacna crocea*, semi-diagrammatic transverse section of animal *in situ* byssally attached within coral rock, exhalant siphon above, gape with emerging byssus below, also paired byssal (pedal) retractors. Hypertrophied *inner* mantle folds (black) above exposing contained zooxanthellae to light; equally hypertrophied *middle* mantle folds (broken lines) below, extended to provide chemical assistance in boring (based on Yonge, 1981a). FIG. 3. Semi-diagrammatic section through valve of leptonacean *Phlyctaenachlamys* showing its enclosure within the extruded middle mantle fold, inner fold also enlarged (after Popham, 1939).

the sensory functions of a head by way of chemoreceptive or tactile tentacles and also eyes in the Pectinacea and Limacea, with greatest complexity in the anomalodesmatan *Laternula* (Adal & Morton, 1973). The exception, discussed later, is in the Cardiacea, where eyes occur on the inner folds.

In various bivalves, the middle folds extend outside the shell, causing major changes in habit. They may hypertrophy to assist the valves in rock boring. All species of *Lithophaga* (Mytilacea) penetrate calcareous rock, culminating in those species that bore into living corals (Morton & Scott, 1980). Although the boring is shaped by the byssally attached shell, the rock is initially softened by anteriorly protruding middle folds (*not* inner as earlier stated (Yonge, 1955)) which secrete a presumably calcium-chelating mucus (Jaccarini et al., 1968). Species boring into living coral also possess posterior glandular areas, their secretion considered to prevent overgrowth of the boring by the coral (Morton & Scott, 1980).

The Tridacnidae (Cardiacea) demand special attention. During evolution (*not* during development, when of necessity the final form is quickly attained) the mantle/shell turned through an angle of some 180° in the sagittal plane in relation to the byssally attached visceropedal mass (Yonge, 1953b). The umbones are thus situated midventrally, immediately anterior to the enlarged byssal gape (Fig. 2). The anterior adductor is lost. The siphons, solely composed of inner folds bearing modified eyes (Stasek, 1966), occupy the entire upper surface and are enormously enlarged to house and expose to the light a vast population of endosymbiotic dinoflagellate zooxanthellae. On the under surface, the middle folds are enlarged and protrude to assist by chemical means the mechanical action of the massive valves in excavating a shallow depression in the invariable substrate of dead coral rock. Together with adventitious additions to the rim of the byssal gape by the outer folds, this excavation ensures intimate contact between shell and substrate so preventing any entrance of even the smallest predators which could destroy the delicate pallial organs (Yonge, 1981a).

Such is the condition in *Tridacna maxima* and *T. squamosa*, while in the smaller *T. crocea* the ventral middle folds and the posterior pedal (byssal) muscles (rocking the downward grinding valves) are further enlarged to achieve full penetration. Massively attached below, the richly pigmented inner folds spread widely over the rock surface above. In the "giant" species (*T. gigas, T. derasa* and the related *Hippopus hippopus*), byssal apparatus and gape are lost during growth, with posture finally maintained by virtue of the weight of the enormously thickened umbonal region of the valves (Yonge, 1981a).

Fungiacava eilatensis (Mytilacea) penetrates, pedal side uppermost, into the skeleton of the hermatypic coral, *Fungia scutaria* (Goreau et al., 1969). The enlarged inhalant siphon opens into the coelenteron, the two animals with the zooxanthellae in the coral living in three-way symbiosis (Goreau et al., 1970). The middle folds protrude and unite, entirely enclosing the very delicate shell. Penetration of the calcareous skeleton can only be by the agency of this pallial covering (Goreau et al., 1972).

Similar partial or total enclosure of the valves by the united middle folds (Fig. 3) occurs in the largely commensal Leptonacea (Erycinacea), particularly in the Galeommatidae, with progressive reduction of the shell (but *not* of the mantle) in the series *Galeomma/Ephippodonta/Phlyctaenachlamys/Chlamydoconcha* (Morton, 1981b). Forming the outer covering of these delicate animals, the middle folds have acquired a protective role, some carrying autotomizing and probably poison-containing tentacles, while in *Galeomma polita* (Morton, 1973a) large tentacles project in an apparent dymantic display. In *G. takii* (Morton, 1973b), the young are protected among defensive papillae dorsally.

In *Lima hians* (Limacea), the long, bright yellow and non-retractile middle fold tentacles assist by "rowing" the swimming movements, which Gilmour (1967) associates with nest-formation in these unusual bivalves. The flexibility needed in these movements explains their uniquely complex structure. Each tentacle is subdivided by septa at the level of any one of which it may autotomize. Again protection is chemical, a distasteful mucus produced by epidermal glands.

The sand grains which encrust the shell surface in various of the Anomalodesmata are attached by secretions from arenophilic glands. In *Periploma*, these originate in the middle folds (Morton, 1981a) but, in *Entodesma*, Prezant (1981) stated that they open under the periostracum, i.e., on the outer lobe, through which the secretion passes. But it seems probable that all such glands originate in the middle folds. In the Veneracea the middle folds are duplicated (Ansell, 1961).

The inner folds are muscular and they control the increased water flow. Their radial muscles (Fig. 1) are attached to the valves along the pallial line so that lateral compression inevitably produced cross-fusion at each end with creation of the adductor muscles. Like the ligament which opens the valves, these are of pallial origin; they are *not* modified shell muscles.

Apart from the uniquely specialized Tridacnidae, inner folds are most enlarged in the Pectinacea, forming the velum or pallial curtains. Their local apposition separates inhalant and exhalant regions. Areas of separation direct the jets produced by contractions of the enlarged region of quick muscle in the solitary adductor. This enlargement was initially due to the need for cleansing the under (right) half of the mantle cavity in these pleurothetic bivalves (Yonge, 1936). With loss of byssal attachment, these sudden ejections came to produce the "escape" and "swimming" movements exhibited by the stream-lined scallops, species of *Chlamys* (Moore & Trueman, 1971), *Pecten* (Thayer, 1972) and *Amusium* (Morton, 1980). Pallial curtains are largest in the abyssal, possibly carnivorous, Propeamussidae (Knudsen, 1970). All have a filtering fringe of "guard" tentacles distinct from the longer and extensile "exploratory" tentacles which, with eyes (except in the Propeamussidae), surmount the middle folds (Waller, 1972).

Conditions differ in the Arcoida. As shown in a variety of species by Morton (1978, 1982) and Waller (1980), there are *two* outer folds, the more distal one secretory, the other one

carrying simple photoreceptors beneath the periostracum. Waller considered that a middle fold is lacking with the inner fold sometimes duplicated, but Morton (1982) thought that both are present with the middle fold (devoid of sensory functions) often reduced. Waller found evidence here against the existence of a basic three-fold pattern in the Bivalvia but, as noted elsewhere (Yonge, 1982b), duplication of the outer folds further emphasizes the distinctive characters of the Arcoida.

Early evolution involved conquest, by the Bivalvia, of the superficial infaunal habitat. Neotenic retention of the larval byssal apparatus next permitted epifaunal exploitation (Yonge, 1962b). One result of byssal attachment was anterior reduction (of positive advantage by raising the posterior inhalant opening higher above the substrate), with change from the original isomyarian to a heteromyarian condition (as in the Mytilacea (Yonge & Campbell, 1968)) leading on to pleurothetic monomyarians (Yonge, 1953a). These had a secondary amphidetic ligament and the viscera were reorganized in the sagittal (now horizontal) plane around the central pallial pillar of the adductor.

In the Pectinacea, with right valve undermost, byssal (i.e., pedal) attachment either is retained – even enlarged in species associated with corals (Yonge, 1981b) – or, in scallops, gives place to freedom, or else to cementation (pallial attachment) in *Hinnites* and *Spondylus* (Yonge, 1979). Although viscera and foot are very similar in these genera, hinge and ligament are totally dissimilar (Yonge, 1973), providing further convincing evidence of the separate identities of the viscero-pedal mass and mantle/shell. Throughout, the foot persists as a means of cleansing. In the byssally cemented Anomiacea, it regains its primary function in the crawling *Enigmonia* (Fig. 4) although not in the also unattached, although immobile, *Placuna* (Yonge, 1977). In the Ostreacea, cemented by the left valve, the foot is lost as it is in the very different Plicatulidae and Dimyidae, both attached by the right valve (Yonge, 1978c).

These major changes were unaccompanied by any attachment between opposing mantle margins, which remained free as in modern Nuculacea, Arcoida and Pterioida. Union was delayed until the Mesozoic when, as emphasized by Stanley (1968, 1970), there was a second evolutionary radiation, notably of deep burrowing bivalves. Fusion involved successively that of inner, middle and then the inner surface of outer folds, with accompanying formation of different types of siphons (Yonge, 1957).

The originally suggested categories have now been simplified (Yonge, 1982b) to cover (A) union of inner folds only with separate siphons; (A+) the special case of the Cardiacea where sense organs are carried on the inner folds, the middle folds usually greatly reduced; (B) addition of the middle folds, this now including the Pholadidae; (C) also including the periostracal groove. Previously suggested fusion involving the outer surface of the outer folds and thus union of the outer calcareous layer only occurs "supradorsal" to the ligament in the upper (left) valve of the Anomiidae, most strikingly in the bivalve "limpet" *Enigmonia* (Fig. 4).

Fusion involving the periostracal grooves, or certainly of their secretions, has a major effect on the primary ligament, which in many superfamilies is secondarily extended by fused periostracum (initially misleadingly termed "fusion layer"). This may occur at one end (normally posterior as in *Pinna* where first described (Yonge, 1953c)) or at both ends (Fig. 5B). This provides greater attachment between the valves with reduction in the now less needed teeth (e.g., in Saxicavacea (Yonge, 1971)), but the primary ligament remains solely responsible for valve separation.

A major contribution to bivalve success was the move from anterior to posterior end of the inhalant aperture to be sited ventral to the exhalant opening where, in the septibranch Cuspidariidae, its siphon even becomes adapted for sizing animal prey (Reid & Reid, 1974). This posterior enlargement led to the originally antero-posteriorly symmetrical amphidetic ligament (Fig. 5A) becoming opisthodetic, the posterior outer layer enlarged, the anterior one reduced or lost (Fig. 5B, C). Such ligaments are "external", arching dorsally with the pivotal axis running along the plane of contact between the inner layer and outer posterior

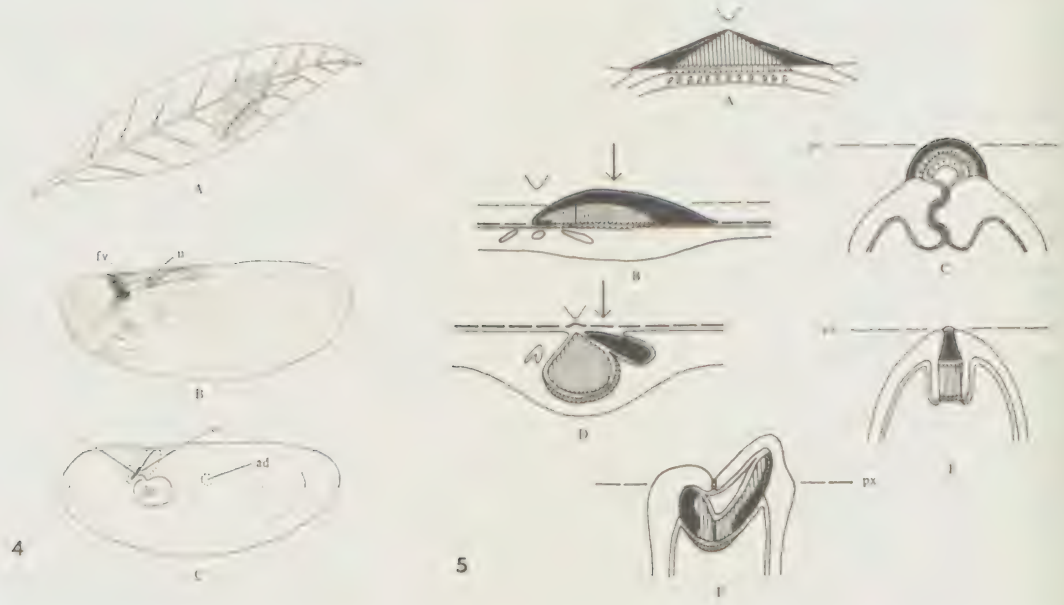

FIG. 4. *Enigmonia aenigmatica* (ca. 30 mm long). A, *In situ* on mangrove leaf showing extended foot; B, upper (left) valve showing position, at apex, of umbo (u) separated from margin by length of fused "supradorsal" valve (fv), ligament lies beneath umbo; C, upper surface of under valve showing position of ligament (l) at end of jutting crurum (cr) posterior to the deep byssal notch (bn), also of reduced adductor (ad) (from Yonge, 1977). FIG. 5. Diagrams of ligamental structure, inner layer with underlying mantle isthmus indicated by vertical lines, outer layers black, periostracal extensions and secondary ligament by thick broken lines. A, "Ideal" amphidetic ligament with taxodont dentition; B, opisthodetic ligament with secondary extensions and heterodont dentition; C, transverse section at arrow in B, hinge plate with tooth (t) and socket (s); D, "internal" ligament (e.g., Mactracea), condensed primary ligament and hinge plate extended ventrally, anterior outer layer lost, secondary ligament occupying pivotal axis (px); E, transverse section at arrow in D; F, transverse section showing separate primary and secondary ligaments in *Plicatula* (after Yonge, 1978a).

layer (Fig. 5C). When the adductors contract, the former layer is compressed with the latter suffering tensile stress, the one a resilium, the other a tensilium.

In various superfamilies, the hinge plate and condensed primary ligament extend ventrally displacing the reduced cardinal teeth, while above the anterior and posterior periostracal extensions unite between the umbones. The valves are now completely united dorsally by the periostracum, which forms a *secondary ligament* (Fig. 1D,E) (Yonge, 1978a). Centrally, this may consist solely of periostracum, the secreting epithelia not united, and primary and secondary ligaments joined dorsally. This is the case in the Lyonsiidae and related Pandoracea (Yonge & Morton, 1980), and also in the Mactracea (Fig. 1C) and Myacea (Yonge, 1982a). Where these epithelia *do* overarch the primary ligament, the secondary ligament is separate as in *Placuna* (originating from byssally cemented Anomiacea), in *Plicatula* (Fig. 1F) and the Dimyidae (Yonge, 1973, 1977, 1978c). In all, the primary ligament forms a resilium, the secondary ligament, attached along the pivotal axis, ensuring valve alignment and possibly providing some tensile force.

The "inner" and "outer" ligaments of conchology are often the inner and the outer (usually posterior) ligament *layers*. The differences between "external" ligaments (as in Veneracea and Cardiacea) and the "internal" ligaments described above are due to ventral extension of the hinge plate and primary ligament with periostracal union dorsally.

The mantle margins may split the primary ligament with major effects on both form and habit. In most bivalves, form is the resultant of radial and transverse growth components, the former radiating out from the umbones and acting in the plane of the generative curve, the latter at right angles to this. As shown by Owen (1953) in *Glossus (Isocardia)*, the former may be deflected anteriorly by a third, tangential, component. Dorsally, this acts in a posterior direction so splitting the entirely primary ligament, with separation of the anterior-facing (prosogyral) umbones and conversion of each valve from a logarithmic planospiral into a corresponding turbinate spiral. Separation of the umbones is accompanied by division of the epithelium secreting the anterior outer ligament layer and anterior regions of the mantle isthmus. The ligament is correspondingly extended at the posterior end.

In the similarly growing, but cemented, Chamacea (Yonge, 1967), where the attached valve (right *or* left) has a large transverse component but the upper one none, the tangential component produces an inverted "gastropod" with deep half turbinate under valves and flat "opercular" upper ones. In striking evidence of the different symmetries involved, although species (possibly individuals) cement by either side, the hinge is that of an upper or lower valve; irrespective of whether this be right or left, the one is the mirror image of the other (Fig. 6), this an apparent result of cementation (Yonge, 1979).

Presence of a tangential component explains the diversity of form displayed in the similarly cemented and normal or inverse Mesozoic Hippuritacea (Yonge, 1967), culminating in the Hippuritidae and Radiolithidae with massive cone-shaped under valves and flat upper ones. All trace of coiling is lost, the completely divided, now vertical, ligament is functionless. Such rudists formed reefs, their height probably lifting them clear of sediment but also ensuring their later destruction.

The effect of a tangential component where a secondary ligament is present in *Cleidothaerus* (Yonge & Morton, 1980) is to obliterate anterior and posterior outer ligament layers and so separate an external (secondary) ligament from an internal (primary) one, here reduced to the inner layer secreted by an isolated island of mantle isthmus. The calcareous lithodesma which in related bivalves occupies the central area of the inner layer, offsetting the effects on this of diverging chondrophores, is, in further consequence of the tangential component, here wrapped around this layer.

In the cemented, freshwater Etheriidae (Unionacea) (Anthony, 1907; Yonge, 1962a), the mantle plays a no less impressive role in the control of form and habit, the animals adapted for life in rushing waters and most strikingly in the South American (Colombian) *Acostae*

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FIG. 6. Chamacea. Hinges (ligament and teeth) of shells attached by right and left valves, mirror images the one of the other, i.e., under and upper, *not* right and left, valves resembling each other (from Yonge, 1967). FIG. 7. *Acostaea rivoli*, inner surface of valves, cemented (here right) valve on left with attached first-formed regions (x) of *both* valves including original ligament. Final position of three layers of typically unionid primary ligament (aol, il, pol) shown, also solitary adductor scar (ad) (from Yonge, 1978b).

(Yonge, 1978b). The post-larva apparently attaches laterally in rock depressions, anterior end downward. Later growth can be only in a posterior, initially upward, direction. Conformity with the substrate then demands a bending in the long axis of the valves which necessitates formation of a new hinge. This is accomplished by movement of the epithelia secreting the typically unionid primary ligament and loss of the most anterior regions, especially of the mantle/shell. The animal becomes monomyarian in a unique manner. The foot is lost in all Etheriidae.

The under, cemented valve incorporates the anterior regions of *both* post-larval valves (Fig. 7). Here, as in the related isomyarian *Etheria*, cementation with its subsequent major effects is entirely a matter of the individual. Settlement is indifferently right or left, solely dependent on which side the post-larva chances to come to rest and then cement itself. What may happen in some Chamacea invariably happens in all Etheriidae: pallial asymmetry is dependent on ontogeny.

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TOXICITY OF COPPER TO GASTROPODA WITH NOTES ON THE RELATION TO THE APPLE SNAIL: A REVIEW

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ABSTRACT

The authors needed to evaluate the toxicity to apple snails (*Pomacea paludosa*) of copper compounds, which were implicated in the snails' declining status on the Loxahatchee National Wildlife Refuge in southern Florida. This species is the sole food item of the endangered Everglade kite. It was considered likely that information generated by investigators attempting to control snails (schistosome fluke hosts) might be useful to investigators attempting to protect snails. Information on 10 species shows that copper is toxic to snails at lower concentrations that that applied in aquatic exotic weed control where the need to protect the apple snail is critical.

INTRODUCTION

The decline in population of the apple snail (*Pomacea paludosa* (Say)) in the deep water habitat (i.e., canals) surrounding the Loxahatchee National Wildlife Refuge in southern Florida has been recognized since the early 1970s. The apple snail is an important link in the food web relationships of the marsh and is the sole food of the endangered Everglade kite, *Rostrhamus sociabilis plumbeus* Ridgway (Stieglitz & Thompson, 1967). It is also an important staple in the diet of other marsh species such as the snapping turtle, *Chelydra serpentina* (Linnaeus); American alligator, *Alligator mississippiensis* (Daudin); boat tailed grackle, *Cassidix mexicanus* (Gmelin); white ibis, *Eudocimus albus* (Linnaeus); and limpkin, *Aramus guarauna* (Linnaeus) (Kushlan, 1975). Consequently, the cause of the decline in the apple snail population needs to be determined to facilitate the management objectives of the refuge.

Copper used in combination with diquat (6,7-dihydrodipyrido[1,2-a:2′,1′-c]pyrazidiinium dibromide) for the treatment of hydrilla (*Hydrilla verticillata* Royle) in the canals surrounding the refuge since the early 1970s may be responsible for the dwindling apple snail population. The population at the refuge appeared normal before 1970 but declined thereafter following applications of copper-containing herbicides at a concentration of 1 mg/l of copper (Martin, per. comm., 1978)[1].

Several crustacean and fish species have been exposed to copper compounds to determine the concentrations which will adversely affect their survival, growth, behavior and reproduction (Anonymous, 1976). However, few such studies have been done on valuable freshwater molluscs. Copper and copper-based pesticides have well-documented molluscicidal capabilities and have been used extensively to eradicate snail populations in countries plagued by schistosomiasis, a disease caused by trematodes that use certain species of snails as an intermediate host. The information compiled by investigators attempting to control these snail populations may be useful in assessing the impact of copper on the apple snail, provided the appropriate environmental ranges of the environmental variables were provided in the studies. (Paulini (1974) prepared a review similar to this one but with a different focus and emphasis.)

GENERAL TOXICITY

Ravera (1977) was able to kill *Biomphalaria glabrata* (Say) with copper sulfate at 0.1 mg/l

[1] Refuge Manager, Loxahatchee National Wildlife Refuge, Florida.

copper in 47 hours (ST_{50}). When Hoffman & Zakhary (1953) exposed *B. boissyi* (Potiez & Michaud) to copper sulfate at 20°C for 72 hours, 38% died at 1.3 mg/l copper sulfate.

Arthur & Leonard (1970) found that 14.8 μg/l Cu at pH 7.1-8.2 was toxic in 6 weeks to the snails *Campeloma decisum* (Say) and *Physa integra* (Haldeman). Chronic 30, 60 and 120 day tests with *Biomphalaria glabrata* revealed 18, 28 and 38% mortality at 0.013, 0.0026 and 0.0026 mg/l copper, respectively (Cardarelli, 1974).

FACTORS AFFECTING TOXICITY

Life stage

Frick et al. (1964) exposed *Biomphalaria glabrata* to cuprous oxide and found a 24-hour LC_{50} of 0.4 mg/l for adult snails and 0.31 mg/l for juveniles. Hopf et al. (1963) found that cuprous oxide had an LC_{50} of 2.2 mg/l at pH 5.2 in 24 hours with adult *B. glabrata*, but only 0.14 mg/l with young snails.

Temperature

Hoffman & Zakhary (1951) obtained a 24-hour LC_{50} of 0.25 mg/l $CuSO_4$ with *Biomphalaria boissyi* at 26°C and pH 5.7-6.8. This is compared to an LC_{50} of 13 mg/l at 14°C – a 50-fold variation associated with the 12-degree difference in temperature. At 26°C, there was an 8-17% kill at 0.07 mg/l $CuSO_4$.

Alkalinity

With *Stagnicola emarginata* (Say) and *Physa* spp., the 96-hour TLm^2 of cupric sulfate was 0.083 mg/l at pH 7.8 and 80 mg/l alkalinity (bicarbonate), but only 0.035 mg/l at pH 7.4 and 6.2 mg/l alkalinity (Howard et al., 1964).

pH

Hopf et al. (1963) found that cuprous oxide had a 24-hour LC_{50} of 0.14 mg/l with young *Biomphalaria glabrata* snails at pH 5.2. At pH 8.5, the LC_{50} was 0.4 mg/l. Low solubility copper compounds (cupric carbonate, copper oxychloride and cuprous oxide) had an LC_{50} of 0.05 mg/l and cupric sulfate (high solubility) had an LC_{50} of 0.2 mg/l copper at pH 5.5. However, at pH 8.5, the LC_{50} of cupric sulfate was 0.11 and cuprous oxide was 0.07 mg/l copper.

Sediment

0.25 mg/l $CuSO_4$ applied continuously to form a barrier to snail migration was lethal to *Biomphalaria pfeifferi* (Krauss) in irrigation mud canals in Kenya (Teesdale et al., 1961).

According to Strufe (1968), "Copper sulphate, like other molluscicides containing heavy metals, is rapidly and sometimes heavily absorbed by mud so that it accumulates at the bottom of the treated water." Incidentally, "in weakly alkaline waters it undergoes flocculation with the result that its molluscicidal activity greatly diminishes."

Chu et al. (1968) found that cuprous chloride, which is slightly soluble in water at pH 7.4-7.9, was 100% toxic at 2.0 mg/l copper to *Bulinus truncatus* (Audouin) in 72 hours. There was little acute toxicity in the presence of mud in the laboratory or in the field. Deschiens et al. (1965) completely killed *Biomphalaria glabrata* and *Bu. contortus* (Michaud) at pH 6-7 at 2.5 mg/l. Chabaud et al. (1965) killed *Physa fontinalis* (Linnaeus), *Bu. contortus* and *Lymnaea* sp. completely in a muddy pond at 3 mg/l of cuprous chloride at pH 6-7, compared to 30 mg/l applied by Chu et al. (1968) at pH 7.8-8.0 to *Bu. truncatus*. The copper LC_{50} was less than 1 mg/l at a pH of 6.25 in a turbid field situation (Mozley, 1952); 100 *Bulinus*

[2] Median Tolerance Limit: the concentration of a toxicant at which just 50% of the test animals survive.

(Physopsis) in Southern Rhodesia were added to cages in a pool with 0.37 mg/l dissolved Cu and 0.75 mg/l total Cu. All snails died in 2 days. To summarize, when copper is absorbed in mud it is much less toxic, unless the pH is low.

MODE OF TOXICITY AND SUBLETHAL EFFECTS

Cheng & Sullivan (1977) exposed *Biomphalaria glabrata* at 0.06 mg/l of copper as copper sulfate and found that the osmolality of the hemolymph was lower than that of controls after 12-36 hours of exposure. There was a 20% mortality along with a 40% accumulation of water in the snails. Sullivan & Cheng (1975) had shown major tissue damage to epithelial cells by 0.06 mg/l $CuSO_4$ for 60 hours. Yager & Harry (1964) indicated that the ability of *B. glabrata* to retract into the shell after 72 hours was depressed at concentrations of 0.05-0.10 mg/l copper as copper sulfate and copper nitrate. Oxygen consumption of *B. alexandrina* (Ehrenberg) was lowered by 48% of the normal rate after 48 hours of exposure to 0.5 mg/l $CuSO_4$ (Ishak & Mohamed, 1975). An equally marked effect was observed at 0.12 mg/l for the first 24 hours.

Deschiens et al. (1965) applied cuprous oxide and cuprous chloride as powders of very fine particulate size at 1-2 mg/l. At these concentrations, they were not toxic to other forms of aquatic life, but had a residual molluscicidal effect that lasted up to a year. Colloidal copper and very fine copper powder also were effective as molluscicides. It was concluded that these copper compounds acted variously by contact, penetration or by being ingested. There was a lack of activity against the eggs, which, of course, do not feed. The oyster drill (*Urosalpinx cinerea* (Say)) would not climb up a copper strip (about as wide as the snails' height) for mussel bait at the top (Huguenin, 1977).

Etges (1963) found that copper carbonate, sodium pentachlorophenate (Na PCP), zinc chloride and copper sulfate repelled *Biomphalaria glabrata* in concentration gradients from bait, whereas barium carbonate, zinc oxide and barium chloride did not. The concentrations were 0.003 μg/l for $CuCO_3$, 0.05 μg/l for Na PCP, 0.256 μg/l for zinc chloride, and 0.01 μg/l for $CuSO_4$. Etges concluded "the present data also suggested that *A.* [= *Biomphalaria*] *glabratus* is probably little affected by any residual action of $CuCO_3$ said to be detectable in bottom mud of a stream one year after application. Slight as the solubility of $CuCO_3$ may be, it appears perfectly sufficient to allow *A. glabratus* to perceive and avoid it. Such a molluscicide might remain in a stream bed indefinitely, but never kill a snail when it also acts as a repellent." On the last point, Barbosa (1961) found that *B. glabrata* and *Tropicorbis centimentralis* (Lutz), which can resist desiccation for several months, were absent from five of 13 streams 12 months after normal copper carbonate applications. He found that "mud from three streams brought to the Laboratory at the end of the twelfth month after the application of molluscicide was still effective in killing snails." Brackett (1939) observed *Lymnaea stagnalis* (Linnaeus) feed on lettuce with copper carbonate and then die after 3 days.

Hopf et al. (1963) concluded that "nonionized copper is, in fact, converted to ions after passing into the snail through the alimentary canal or body wall. In that case, the advantage of 'insoluble' over 'soluble' copper compounds in mollusc control would lie in greater persistency and greater availability to bottom-living creatures, rather than in a different mode of action. It would seem to make little difference what the source of sparingly soluble copper is. At pH 6.5 there might be insufficient soluble copper available to affect free swimming fish, while the bottom-living and bottom-feeding snails would take up enough to be killed. At the low pH employed by us there is sufficient copper ion in solution to kill both."

CONCLUSION

This information concerning the toxicity of copper to 10 species in four families (Physidae, Lymnaeidae, Planorbidae, Viviparidae) of snails should be used as an impetus to stop or

at least reduce the use of copper for aquatic weed control in and around the Loxahatchee National Wildlife Refuge, where the need to protect the apple snail is critical. Copper is toxic to snails at concentrations of less than 1 mg/l (the concentration applied at the refuge) under conditions of pH (5.9-8.5), temperature and alkalinity (32-192 mg/l) commonly found on the Loxahatchee National Wildlife Refuge. The variable results with sediment may have to do with repeated exposure of sediment to copper. It is hoped that ongoing investigations by the Fish and Wildlife Service will further clarify the relation of these factors with the application of copper-containing herbicides on the refuge.

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DISTRIBUTION AND HABITATS OF SIX SPECIES OF FRESHWATER PULMONATE SNAILS IN ALGARVE, SOUTHERN PORTUGAL

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ABSTRACT

There are various freshwater pulmonate snails in Portugal that are the known or suspected intermediate hosts of trematode diseases of human and veterinary importance. A survey of aquatic habitats in Algarve, southern Portugal, during 1979 and 1980 yielded the following aquatic pulmonate snails: *Bulinus truncatus contortus* and *Planorbarius metidjensis* (Planorbidae), *Fossaria truncatula* and *Radix peregra* (Lymnaeidae), *Physella acuta* (Physidae) and *Ancylus fluviatilis* (Ancylidae). All of the snails except *B. truncatus contortus* were widely distributed in Algarve. *B. truncatus contortus* was found at only one locality. None of the snails were found to be naturally infected with trematodes in this survey, although *Pl. metidjensis* is believed to be the natural intermediate host of *Schistosoma haematobium* in Portugal, and *F. truncatula* is the snail intermediate host of *Fasciola hepatica*.

INTRODUCTION

Several species of Portuguese freshwater snails are known to be of medical and veterinary importance. For example, *Planorbarius metidjensis* (Forbes) has been implicated in the transmission of *Schistosoma haematobium* (Bilharz) in Algarve, southern Portugal (França, 1923; Azevedo et al., 1948), and it has been found susceptible to a strain of *S. bovis* (Sondino) from Salamanca, Spain (Silva et al., 1977). *Bulinus truncatus contortus* (Michaud) has been shown to be susceptible to *S. haematobium* from Angola, Guinea-Bissau and Mozambique (Azevedo & Xavier, 1969; Oliveira et al., 1974). *Fossaria truncatula* (Müller) is the intermediate host of *Fasciola hepatica* (Linnaeus) (Xavier et al., 1965). Therefore, a knowledge of the geographical distribution and habitats of freshwater snails in Portugal, and especially those of medical and veterinary significance, is very important.

MATERIALS AND METHODS

Aquatic pulmonate snails were collected from 62 freshwater localities (Table 1 and Fig. 1) during April and June, 1979, and February, 1980, in Algarve, southern Portugal. Long-handled metal scoops were used to aid in the collection. Notes were taken in regard to the vegetation, water levels, air and water temperatures, pH, and numbers and relative sizes of the snails in each habitat.

To check for trematode infections, snails were introduced individually into glass vials containing 15 ml of water and placed under a 60 watt lamp for 6 hr during several days. Additionally, some of the snails were dissected.

RESULTS

Six species of aquatic pulmonate snails were found during the survey of freshwater habitats in Algarve. These species were the planorbids *Bulinus truncatus contortus* and *Planorbarius metidjensis*, the lymnaeids *Fossaria truncatula* and *Radix peregra* (Müller), the physid *Physella acuta* (Draparnaud) and the ancylid *Ancylus fluviatilis* Müller. Their distributions are shown in Figs. 2-4. Additionally, unidentified prosobranch snails also were collected from several of the localities (see Table 1 for their distributions).

TABLE 1. List of localities from which freshwater snails were collected.

Localities	Geographical co-ordinates		Altitude (m)	*Pl. metidjensis*	*B. t. contortus*	*F. truncatula*	*R. peregra*	*Ph. acuta*	*A. fluviatilis*	Prosobranchia
	Latitude (North)	Longitude (West)								
1. Alferce 1	37°20′30″	8°29′	325						+	
2. Alferce 2	37°20′	8°29′30″	400	+						
3. Alferce 3	37°20′	8°30′	475						+	
4. Monchique	37°19′	8°34′15″	475					+		
5. Foia 1	37°18′30″	8°36′	680			+	+		+	
6. Foia 2	37°18′30″	8°35′30″	630	+				+	+	
7. Mexilhoeira Grande	37° 9′30″	8°38′	70					+		+
8. Barragem da Bravura	37°11′	8°42′	80	+				+		
9. Alfambras	37°15′30″	8°48′30″	100						+	+
10. Algezur	37°19′	8°48′	80							+
11. Arrifana 1	37°17′30″	8°51′	100	+		+		+	+	
12. Pinhal Novo	37°15′	8°49′	100	+					+	
13. Bordeira	37°12′	8°51′30″	100				+			+
14. Pedralva	37° 7′30″	8°53′	134	+						
15. R. Torre	37° 3′30″	8°55′30″	78	+				+		+
16. Arrifana 2	37°17′30″	8°52′	90	+				+	+	
17. Lagos	37° 6′	8°40′	Sea coast				+			
18. Bensafrim	37° 9′	8°43′30″	100	+				+		
19. Figueira 1	37° 9′30″	8°35′	50				+	+		
20. R. Bensafrim	37° 8′	8°41′30″	95				+	+		+
21. Figueira 2	37° 4′30″	8°50′30″	93	+						+
22. Boina	37°10′30″	8°32′	67	+			+	+		
23. Porta de Lagos	37°15′	8°32′30″	94	+						
24. R. Odelouca 1	37°12′30″	8°30′30″	100					+		+
25. R. Odelouca 2	37°11′30″	8°29′	100			+				
26. R. Falacho	37°11′30″	8°28′	100						+	
27. R. Arade (Silves)	37°11′30″	8°26′	100	+		+	+	+		+
28. R. Alcantarilha	37°10′30″	8°21′	60	+				+	+	
29. R. Alte (Boliqueime)	37° 7′30″	8° 9′	56				+	+	+	+
30. R. St. Lourenço (St. Lourenço)	37° 4′30″	7°59′	30	+				+		
31. Faro	37° 2′	7°55′	Sea coast	+			+	+		
32. R. Pechão	37° 2′	7°52′	Sea coast			+	+			
33. R. Marim	37° 3′	7°49′	Sea coast			+	+	+		

TABLE 1. (Continued)

Localities	Geographical co-ordinates		Altitude (m)	*Pl. metidjensis*	*B. t. contortus*	*F. truncatula*	*R. peregra*	*Ph. acuta*	*A. fluviatilis*	Prosobranchia
	Latitude (North)	Longitude (West)								
34. R. Tronco (Fuseta)	37° 4′	7°45′30″	Sea coast	+		+		+		
35. R. Mosqueiros (Livram.)	37° 5′	7°43′30″	22	+		+	+	+		
36. R. Cacela (Cacela)	37°10′	7°33′	26	+				+	+	
37. Junqueira	37°16′30″	7°29′	45	+						
38. Castro Marim	37°13′30″	7°27′	41					+		+
39. Marmeleiro	37°27′	7°30′	207	+					+	
40. R. Odeleite (Odeleite)	37°20′	7°30′	130			+		+	+	
41. Amaro Gonçalves (Fundo)	37° 6′	7°44′	40	+		+		+	+	
42. Moncarapacho	37° 5′	7°47′	60	+				+	+	
43. R. Arroio (St. Cat. F. Bispo)	37° 9′	7°48′	200	+		+				
44. R. Arroio (Carrasqueira)	37° 9′30″	7°49′30″	250	+		+				
45. R. Rio Seco (Estoi)	37° 6′	7°54′30″	95	+		+	+	+		
46. R. Odeleite (Montes Novos)	37°16′	7°55′	450			+	+		+	
47. R. Quinta	37°14′	7°59′	375	+					+	
48. R. Algibre (Querença)	37°11′30″	7°59′30″	350						+	
49. Porto Nobre	37°10′30″	8°	325	+		+				
50. Loulé	37° 7′30″	8° 1′	227	+		+				
51. Vale do Lobo	37° 4′30″	8° 4′	36	+				+		
52. Aldeia das Vinhas 1	37° 5′	8° 6′30″	46			+				
53. Aldeia das Vinhas 2	37° 6′	8° 7′30″	46		+	+	+	+	+	+
54. R. Arade	37°17′	8°18′	120			+		+		
55. R. Odelouca (Baião Velho)	37°23′15″	8°20′30″	200						+	
56. R. Foupana (Corte St. Tomé)	37°23′30″	7°31′30″	160	+						
57. Pereiro	37°27′	7°36′30″	260	+				+		
58. R. Poupana (Barrada)	37°25′	7°49′	320	+			+			
59. Odeceixe	37°26′	8°46′	87	+				+	+	
60. Nave	37°16′30″	8°33′	180	+			+	+		
61. R. Alte (Alte)	37°14′	8°13′	160				+	+	+	+
62. Vale de Rosa	37°16′	7°57′	470			+	+		+	

FIG. 1. Algarve localities with freshwater snails. The numbers on the map correspond to those in Table 1.

Bulinus truncatus contortus was found at only one locality (Fig. 2), Aldeia das Vinhas (Station 53), a lake which had connection with a stream. The specimens were found on stones, aquatic vegetation and mud. Water temperature at this locality at the times the snails were collected was 21°C, and the pH of the water was 7.0.

Planorbarius metidjensis (Fig. 2) was found in ponds, tanks, fountains, small pools, brooks, rivers and dams. Water temperature ranged from 12-22°C and pH from 4.5-8.0. Some of

FIG. 2. Distribution of *Planorbarius metidjensis* (■) and *Bulinus truncatus contortus* (○) in Algarve.

the samples were found in slightly polluted water and most of the habitats had total or almost complete sun exposure. A consistent feature about the localities in which this species was found is that in all of them the water was either gently flowing or was more or less static. *P. metidjensis* normally was found on aquatic vegetation and on rocks, but it also was often found on mud in shallow water, on walls of tanks and fountains, and floating on surface water. Its eggs were found on aquatic vegetation, on rocks and on shells. The snails were particularly abundant near points of human contact (for example, at places where clothes are washed).

Fossaria truncatula (Fig. 3) normally was found in gently moving water in brooks and rivers, but it also was sometimes found in small ponds near river banks. Water temperature of its habitats ranged from 13-22°C, and the pH ranged from 6.0-7.5. In these habitats, the species was found in shallow water, usually on stones, aquatic vegetation or mud. Some of the specimens were found just out of the water, crawling on mud and on sheltered parts of the grass situated along the water's edge.

Radix peregra (Fig. 3) was found in water either gently flowing or more or less static, in tanks, fountains, field-drains, brooks, small ponds near river banks, rivers and dams. Water temperatures of their habitats ranged from 13-22°C, and the pH ranged from 6.0-7.5. The snails normally were found on stones, aquatic vegetation or on muddy or sandy bottoms, but they also were found floating on surface water.

FIG. 3. Distribution map of *Fossaria truncatula* (●) and *Radix peregra* (◇) in Algarve.

Physella acuta (Fig. 4) occurred in water either more or less static or slowly flowing. It was found in tanks, fountains, brooks, rivers, small pools and ponds near river banks. Water temperatures ranged from 13-22°C, and the pH ranged from 4.5-8.0. The snails were found on walls of tanks and fountains, on aquatic vegetation, on stones and on mud. They also were often found floating on surface water.

Ancylus fluviatilis (Fig. 4) was found in rivers and brooks in flowing water. Water temperatures ranged from 13-22°C, and the pH varied from 4.5-7.5. The limpets were found on stones.

FIG. 4. Distribution map of *Physella acuta* (♦) and *Ancylus fluviatilis* (□) in Algarve.

The prosobranch snails collected during the survey were found in slowly flowing water in brooks and rivers. Water temperatures ranged from 15-22°C, and the pH ranged from 6.0 to 8.0. The snails were found on aquatic vegetation, stones, muddy or sandy bottoms.

None of the freshwater snails collected during the survey were found to be infected with trematode parasites.

DISCUSSION

The present study confirms the report of Nobre (1941) that *Planorbarius metidjensis*, *Fossaria truncatula*, *Radix peregra* and *Physella acuta* occur in Algarve, and gives much greater detail about their distributions. In the present survey, *Bulinus truncatus contortus* was found at one site only. *B. truncatus contortus* was found by Nobre only in northern Portugal, not in Algarve; other authors (Bettencourt et al., 1921; França, 1923; Azevedo et al., 1948) also did not find *Bulinus* in Algarve, even though vesicular schistosomiasis was found in some localities in Algarve. However, Azevedo & Xavier (1969) and Oliveira et al. (1974) mention working with *B. contortus* from Silves (Algarve). In their papers, Bettencourt et al. (1921) and França (1923, 1924) indicated that *Pl. metidjensis* was the intermediate host of *Schistosoma haematobium*. Bettencourt & Borges (1922) demonstrated experimentally that *Pl. metidjensis* from Algarve was infected in nature with *S. haematobium*, and Azevedo & Colaço (1950) demonstrated that *Pl. metidjensis* from Algarve was susceptible to *S. haematobium* from Algarve which had been derived from persons with urinary schistosomiasis acquired in Algarve.

The mention by Azevedo & Xavier (1969) and Oliveira et al. (1974) of studying *Bulinus contortus* from Silves (Algarve) is of more than passing interest. However, in spite of our intensive search, *B. truncatus contortus* was not found there, only *Physella acuta*, *Planorbarius metidjensis*, lymnaeids and some prosobranchs. *B. truncatus contortus* may have disappeared later due to alterations in the habitat or from competition from other species. It should be noted that at present the river at Silves is polluted. It also should be mentioned that Nobre (1941) reported *B. contortus* from areas in northern Portugal, where it also has now been

replaced by *Ph. acuta*. Concerning the *B. truncatus contortus* collected in our survey, it possibly may have been introduced in that lake by aquatic birds or through aquatic vegetation.

In terms of parasitology, in our search the snails *Planorbarius metidjensis, Bulinus truncatus contortus, Fossaria truncatula, Radix peregra* and *Physella acuta* were not found to be infected with trematodes. However, from our limited observations, it cannot be concluded at present that no trematode infections occur in Algarve. More detailed investigations are needed to determine that.

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MORPHOLOGICAL AND BIOCHEMICAL STUDIES ON AN AQUATIC PULMONATE GASTROPOD, *RADIX QUADRASI*, IN THE PHILIPPINES[1]

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ABSTRACT

A total of 1,712 snails collected from 11 different areas in the Philippines and identified as *Radix quadrasi* were studied morphologically. Four shell shapes were observed, namely, oval, semi-oval, oblong and oblong-elongate. While the first three occurred either singly or mixed in 10 areas, the oblong-elongate type was found in only one area, San Jose. The total protein content in the whole body extract and hemolymph increased as the snails grew to size 14 mm, beyond which the total protein content levels were reduced. However, size (age) did not affect the qualitative pattern of the separated proteins. Total protein content of the whole body extract and hemolymph of uninfected snails was observed to differ from the infected ones. Electrophoretic analysis revealed the presence of a maximum number of 16 protein fractions from the whole body extract and hemolymph. There were, however, slight variations in the protein patterns of the whole body extract and hemolymph among samples from the different areas. The consistent absence of one or more of the protein fractions served as the basis for grouping the snails from the various geographic areas into five different groups. The snails from San Jose exhibited not only a distinct shell shape but also a protein pattern separable from those of the other areas.

INTRODUCTION

The Lymnaeidae are common freshwater snails found in nearly all parts of the world. They are found inhabiting varied habitats like grassfields, kangkong fields, ricefields, ditches, canals, slow-flowing streams, stagnant pools, swampy areas and other muddy places, including man-made pools with aquatic vegetation. In the Philippines, they prefer habitats with standing water.

Three species of Lymnaeidae are generally believed to occur in the Philippines. The first species known to be endemic in the Philippines was named by Pfeiffer (1845) as *Amphipeplea cumingiana*. This species was called *"Myxas" cumingiana* by Bequaert & Clench (1939), *"Lymnaea" cumingiana* by Hubendick (1951) and *"Mixas" cumingiana* by Velasquez (1971).

A second species was named *Lymnaea philippinensis* by Nevill (1881). Bequaert (cf. De Jesus, 1935), De Jesus (1935), Manipol (1936), De Jesus & Mallari (1938), Bequaert & Clench (1939), Velasquez (1971) and Malek & Cheng (1974) used Nevill's species name, identifying their specimens from Nevill's original description. Abbott (1948) considered *Lymnaea philippinensis* Nevill to be a synonym of "*L. (Fossaria) ollula* Gould (= *L. pervia* Martens)", a species previously known from China and Japan, and Hubendick (1951) considered all three of the above nominal species (*philippinensis, ollula* and *pervia*) to be synonyms of *L. viridis* Quoy & Gaimard, a species originally named from Guam.

A third species was named by Möllendorff (1898) as *Lymnaea quadrasi*. This species was identified as *Radix swinhoei* (Adams) by Nevill (1881), Manipol (1936), Abbott (1948), Velasquez (1971) and Clarke (1978, pers. comm.). Tubangui (1932) identified this same species as "*Lymnaea peregra* Muller". Bequaert & Clench (1939) referred to it as *Lymnaea (Radix) swinhoei* var. *quadrasi*. Hubendick (1951) considered *swinhoei* as a geographical

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strain of *L. auricularia* Linnaeus and included the Philippine specimens in "*L. auricularia swinhoei* Adams". Hubendick (1951; 1978, pers. comm.) described another strain from the Philippines as "*L. auricularia rubiginosa* Michellin".

Burch's (1980, 1981) classification would place *"Lymnaea" philippinensis* in *Austropeplea*, *"L." quadrasi* (? = *swinhoei*; ? = *rubiginosa*) in *Radix*, and *"L." cumingiana* in *Bullastra*.

From the above, it appears that morphology alone as a basis of nomenclature presents difficulties. Although there is a considerable morphological uniformity among the Lymnaeidae, there is, however, a wide range of variation within the various species and even within the same population (Hubendick, 1951). Characters supposedly considered diagnostic also are found to vary (Clarke, 1973). Anatomical similarities among species as well as variation within species create a number of unusual taxonomic problems which seem to obscure systematic relationships (Inaba, 1969).

Many workers believe that morphological differences are either preceded by or accompanied simultaneously by an underlying chemical differentiation (Johnson & Wicks, 1959). Indeed, Sibley (1962) has pointed out that a biochemical study of proteins is merely comparative morphology at the biochemical level.

The present investigation aims to compare the electrophoretic patterns of soluble proteins in the local Philippine snail *Radix quadrasi*, using different sizes (ages) from different populations, and to compare protein variation to variation in morphological characters. This work further aims to characterize the electrophoretically separated protein patterns, which might be useful in further studies to clarify systematics and nomenclature in the Philippine Lymnaeidae.

MATERIALS AND METHODS

Collection and maintenance

Samples of *Radix quadrasi* were collected over a period of six months by handpicking from various types of habitats in several localities on Luzon Island, Philippines (Table 1). Voucher specimens have been deposited in the Conchology Section, Department of Zoology, National Museum, Manila. The collected snails were placed in large wide-mouthed bottles containing water and enough soil to keep the snails alive during transport from the sampling sites to the laboratory. The snails were placed in small aquaria or plastic basins under identical laboratory conditions at room temperature. The bottoms of the containers were covered with mud and a small amount of deionized water. A sufficient amount of lettuce or kangkong leaves was used as food. The cultures were aerated daily.

Morphological studies

Morphological examinations and observations were based mainly on the shell characters such as shape, length, width, color and direction of coiling of the shell. To establish morphological differences, if any, within and among populations, further detailed observations were done on the height, nature and distinctness of the spire, the size and shape of the aperture, the length of the aperture in proportion to the length of the spire, the number and shape of the whorls, the shape of the apex, the nature of the sutures, the nature of the outer lip, the shell texture and the presence or absence of distinct growth lines.

For verification of identification, type specimens were sent to Dr. Bengt Hubendick of Naturalhistoriska Museet, Göteborg, Sweden, and Dr. Arthur H. Clarke, at that time at the Smithsonian Institution, Washington, D.C., U.S.A. Only those identified as *Lymnaea (Radix) swinhoei quadrasi* von Moellendorf (Clarke, 1978, pers. comm., using the concept of Bequaert & Clench, 1939) or *L. auricularia swinhoei* Adams and *L. auricularia rubiginosa* Michellin (Hubendick, 1978, pers. comm.) were used in our biological studies. [To us, the shells of *L. a. swinhoei* and *L. a. rubiginosa* appeared to be morphologically identical.] For the purpose of this study, our specimens were given the oldest name specifically applied to this type of lymnaeid snail from the Philippines, i.e., *Radix quadrasi*, since it has not been proven conclusively that our Philippine snails of this type are identical to the Taiwanese *R. swinhoei* or to the East Indian *R. rubiginosa*.

Biochemical techniques

Preparation of the samples. Shell length and total shell-animal weight of laboratory-maintained snails from the different populations were individually measured. The snails were sorted according to shell length (the maximum distance from the shell apex to the anterior rim ("base") of the shell aperture) and

were further classified for variations based on shell characters and presence or absence of trematode parasite infection. Whole body extracts and hemolymph of individual snails were collected as follows.

(a) Whole body extracts. The bodies of the individual snails were separated from their shells by gently breaking the shells and picking the pieces of shell away. The body tissues were weighed, cut into pieces, macerated and examined under the stereomicroscope for the presence or absence of larval trematodes, in order to separate the infected snails from the uninfected ones. Only the uninfected snails were used, unless we were looking specifically for effects of parasitization. Whole body tissues of smaller snails whose shell lengths were 9 mm or less, having exactly the same shell characters, were pooled in groups of two to four. Samples were diluted with Carriker's (1946) physiological saline and homogenized in an improvised hand-operated homogenizer. For every 0.15 g tissue (wet weight, tissue-blotted), 1.0 ml of saline was added (Davis & Lindsay, 1967). A few drops of toluene were added to the mixtures after homogenization to remove lipids (Smith, 1960). The homogenates were centrifuged at 2400 rpm for 15 min, the supernatant minus the toluene was drawn by separate pipettes and placed in microtest tubes for storage at 0°C until used for electrophoresis.

(b) Hemolymph. Hemolymph was collected from individual snails representing the different sizes per population. The snails were first cleaned with distilled water, air dried, then pierced with a hypodermic needle (gauge 25) at the heart region. A capillary tube was inserted into the hole to allow hemolymph to flow up the tube by capillary action (Yoshino & Cheng, 1977). Collection was done immediately after insertion of the tube to avoid the mucus secretion of the foot from mixing with the hemolymph. Both ends of the tubes containing the undiluted hemolymph were sealed with plastic clay and centrifuged for 3 min at 1000 rpm. They were stored at 0°C until used.

Determination of the total protein content. The total protein values of the different whole body extracts and hemolymph were determined by means of the Biuret test. A modified Biuret reagent was used to produce a blue-purple copper complex when added to dilute whole body extracts or hemolymph. The color produced by the samples, which was proportional to the protein concentration, was compared to a standard solution (fetal calf serum) and the total protein values were determined. The Beckman Model 150 Ultramicro Analytical System was used in the determination.

Electrophoretic procedure. The methods of Davis (1967) and the Canalco Research Instructions (1969) for disc electrophoresis were followed. Diagrammatic electrophoretograms were constructed to facilitate the characterization of samples from different areas.

RESULTS

The results of the present study were based on 1,712 snails collected from 11 areas. Of the snails collected, 428 were electrophoretically examined for whole body proteins; 109 were examined electrophoretically for hemolymph proteins; 34 were examined electrophoretically for the effect of infection on the protein pattern; and 203 snails were used for the total protein content determinations of whole body extracts and hemolymph. The rest were observed for their shell characters and measurements.

Morphology

Table 1 shows the size distribution of the 1,712 snails collected from the 11 collecting areas. Sizes ranged from 5 to 23 mm. Examination of the samples from different areas showed that the bulk of the population belonged to the size class 7-16 mm. As observed in 1,506 snails, this size class composed 87.97% of the total collection. Smaller snails of the size class 5-6 mm constituted 2.11% of the collection, and the larger snails of the size class 17-23 mm constituted 9.92% of the collection.

The color of the shell varied from yellow-brown to dark brown to brown tinged with black to pure black. The degree of darkness of the shell was affected by the size (age) of the animal as observed in the laboratory and by the snail's immediate surroundings. The spires were more or less pointed and showed varying heights, ranging from short to tall, with pointed apices sharply demarcated from the body whorl. The whorl sutures varied from shallow to deep. The number of spire whorls varied from three to five. The whorls were convex, rounded, and rapidly increased in size from the shell apex anteriorly. The dorsolateral surfaces of the body whorls were angular. The apertures were pear-shaped, large and broad and longer than the spire. The lateral lips were straight and thin. The columella was either slightly,

TABLE 1. Size distribution of *Radix quadrasi* from the different collecting areas.

Shell length in mm[1]	Metropolitan Manila					Bulacan		Laguna	Batangas	Cagayan	Nueva Vizcaya	Total
	Univ. Philip. Campus, Diliman			San Juan	Parañaque	Sta. Maria	San Jose	San Pedro	Nasugbu	Camalaniugan	Bayombong	
	CAS[2] pool	Lagoon	NSRC[3]									
5	5	–	1	–	2	–	–	–	–	2	–	10
6	9	7	1	–	5	–	–	–	–	4	–	26
7	8	23	16	15	14	6	1	3	7	6	5	104
8	8	38	36	8	16	7	10	6	1	9	6	145
9	10	44	37	16	29	2	7	7	1	7	8	168
10	10	51	49	18	28	16	9	7	3	18	5	214
11	10	57	36	9	11	10	8	6	4	2	17	193
12	7	48	30	9	6	9	8	12	7	36	28	198
13	9	34	15	10	2	14	11	7	5	14	17	138
14	9	23	15	8	7	11	11	2	3	14	26	130
15	13	17	27	1	1	9	15	–	–	19	26	128
16	1	1	12	20	2	6	5	1	7	14	24	93
17	1	1	6	18	1	6	2	–	–	4	9	48
18	1	1	11	18	2	4	–	–	7	5	3	52
19	–	–	9	11	–	2	–	1	–	–	3	27
20	–	–	6	8	–	1	–	–	–	1	1	17
21	–	–	5	10	–	–	–	–	–	1	–	16
22	–	–	3	7	–	–	–	–	–	–	–	10
23	–	–	–	–	–	1	–	–	–	–	–	1
Total	101	345	315	186	124	104	87	52	45	175	178	1,712

[1]Range: 5 = 5-5.9, 6 = 6-6.9, etc.

[2]College of Arts and Sciences pool, near Pavilion 1.

[3]Natural Science Research Center grassfields.

moderately or deeply twisted. A more or less narrow umbilical chink generally occurred. The shells were thin and fragile, mostly smooth and glossy, and some had noticeable growth lines. The common features of the snail shells in this work agree with Hubendick's concept, with slight deviations such as height of the spire, number of whorls in the spire, and some snails possessed body whorls not distinctly offset from the spire. Fig. 1 shows the four shell shapes observed: oval, semi-oval, oblong and oblong-elongate. There were also characters that varied within the same or between different areas. It was observed that among these variable characters there were certain features usually found together in the same individual. For instance, snails with rounded shells had short spires, fewer shorls, shallow sutures, and only slightly twisted columellae. The more slender snails possessed taller spires, a greater number of whorls, deeper sutures, and more strongly twisted columellae.

Variation within samples from the same area also was observed. The snails (all from the campus lagoon) exhibited three of the shell forms shown in Fig. 1 (oval, semi-oval and oblong). However, in San Jose, only the oblong-elongate shell form was obtained. Furthermore, this shell shape was not collected from the other localities.

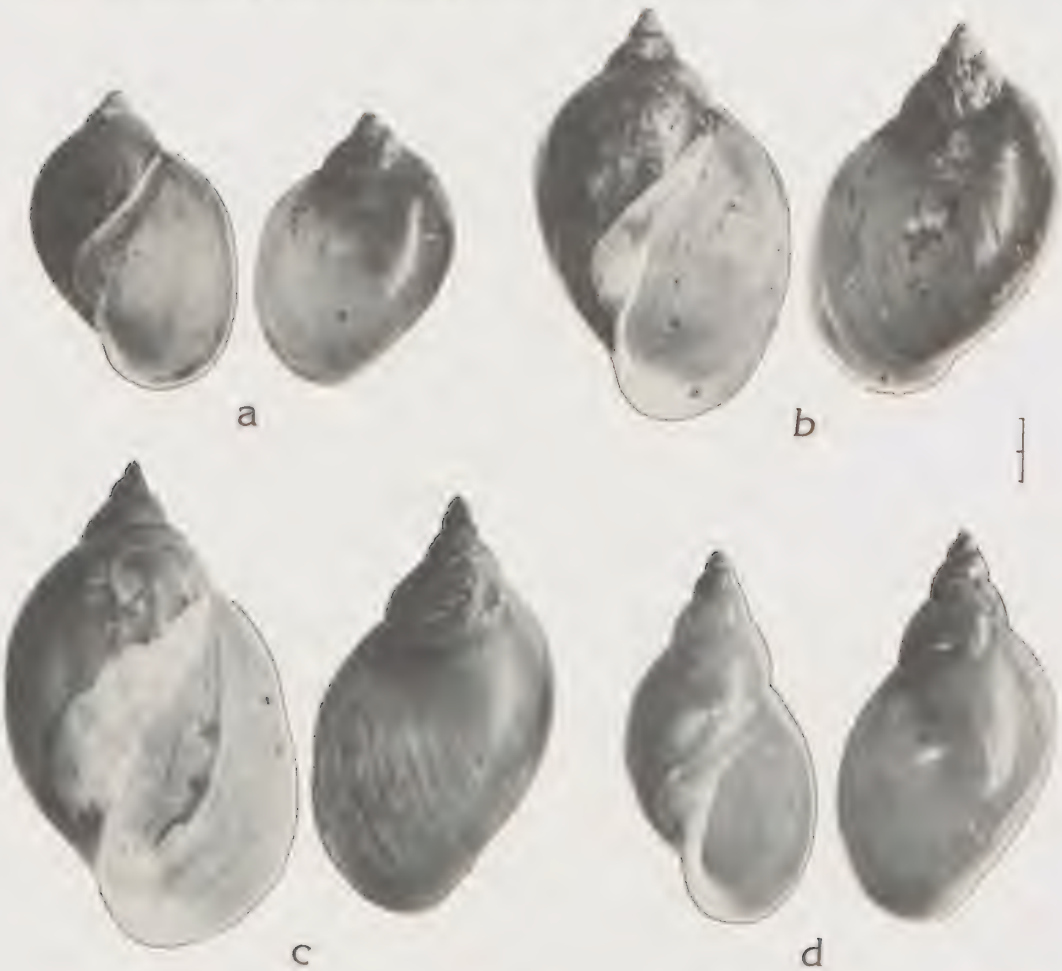

FIG. 1. Different shell shapes observed in *Radix quadrasi*, dorsal and apertural views. a, Oval; b, semi-oval; c, oblong; d, oblong-elongate. Measurement lines in mm.

Total protein

Table 2 shows the total protein concentration (mg per ml of sample) of the whole body extracts (0.15 g/ml saline solution) and hemolymph (undiluted), respectively, from snails of different sizes from the Diliman lagoon. The total protein concentration from both sources increased with body length up to 14 mm, beyond which the total protein concentration levels decreased. (The total protein concentration of the hemolymph was less than that of the whole body extract in snails of the same sizes.) The total protein content of the whole body extract from infected snails was much lower than that of the uninfected ones. In contrast, the hemolymph total protein content was higher in the infected samples than in the normal ones.

TABLE 2. Comparison of the total protein content of the whole body extract and hemolymph between the uninfected and infected *Radix quadrasi* from the University of the Philippines lagoon, Diliman, Quezon City.

Shell length in mm	Total protein content			
	Whole body extract mg/ml (0.15 g WBE/ ml saline solution)		Hemolymph mg/ml hemolymph (undiluted)	
	Uninfected	Infected	Uninfected	Infected
8	0.0630	0.0371	0.0258	0.0397
9	0.0690	0.0483	0.0371	0.0457
10	0.0834	0.0569	0.0431	0.0543
11	0.0889	0.0656	0.0543	0.0656
12	0.1036	0.0776	0.0656	0.0716
13	0.1173	0.0890	0.0742	0.0820
14	0.1208	0.1035	0.0802	0.0932
15	0.0716	0.0656	0.0569	0.0569

Electrophoretic analysis

Whole body extracts. The protein pattern of the whole body extract was based upon the electrophoretic analysis of 428 snails representing different sizes ranging from 6 to 23 mm from the collecting areas. Visual inspection showed a maximum number of 16 distinct protein components, resolved by disc electrophoresis at pH 8.2 to 8.4 in the whole body extract. These proteins, however, were not always resolved in samples from every area nor in all individuals within an area. The protein bands were numbered consecutively from 1 to 16, with band no. 1 nearest the origin and band no. 16 the farthest from the origin, located just behind the tracking-dye band. All 16 bands represented proteins which migrated towards the anode.

Table 3 shows the Rf value range of the protein fractions, which were obtained from the results of three to six runs per whole body extract sample and one to three runs per hemolymph sample. The Rf values were used to support identification of the protein fractions based on visual inspection.

Three to six test runs per individual from each area were made. With the exception of band 13, which showed the most overall mobility (from all individuals tested from all areas), the mean variation of all the bands from all areas did not go beyond 0.045 (Table 4).

TABLE 3. Rf values of the 16 protein fractions separated by disc electrophoresis from *Radix quadrasi*, based on 428 snails, representing different shell sizes ranging from 6 to 23 mm.

Band number	Range of Rf values	Distance variation
1	0.021 - 0.046	0.025
2	0.050 - 0.094	0.044
3	0.096 - 0.133	0.037
4	0.136 - 0.166	0.030
5	0.169 - 0.222	0.053
6	0.224 - 0.288	0.064
7	0.299 - 0.356	0.057
8	0.385 - 0.438	0.053
9	0.451 - 0.512	0.061
10	0.528 - 0.589	0.061
11	0.592 - 0.634	0.042
12	0.654 - 0.716	0.062
13	0.721 - 0.789	0.068
14	0.798 - 0.843	0.045
15	0.860 - 0.919	0.059
16	0.937 - 0.981	0.044

The maximum numbers of protein fractions in snails of different shell sizes are shown in Table 5. Of the 16 protein fractions, bands 3, 4, 6, 10 and 15 were consistently present in snails with shells 10 mm or larger from all populations (Table 6), with the exception of band 4, which was absent in San Jose. Only bands 3, 4 (except San Jose) and 6 were consistently found in all sizes from all collecting areas. In addition to bands 10 and 15 that showed consistent appearances only from snails with shell sizes 9 or 10 mm upward, there were other bands whose appearance was affected by size (bands 2, 7 and 8). The density of the rest of the bands, but not their frequency of appearance, was affected by size. Samples from smaller snails (7 to 9 mm) exhibited thin, lightly stained bands. These variations are thought to reflect the variations in the total protein concentration, as well as in the concentration of the individual protein fractions. Results of this study showed an increasing total protein content of the whole body extract from size 8 to 14 mm, declining at 15 mm (Table 2). Batangas had the greatest percentage of occurrence of consistent bands regardless of size, followed by the Natural Science Research Center grassfields, the Diliman lagoon and Nueva Vizcaya (Table 7). In other areas, there was a lesser percentage of occurrence of consistent bands, with each of the individual areas having characteristic patterns of their own.

From their electrophoretic patterns, five groups of snails may be identified as follows.

Group I is characterized by the presence of all 16 bands and includes snails from the University of the Philippines Lagoon (man-made; containing grasses and kangkong), Natural Science Research Center (grassfield) and San Juan (kangkong field).

Group II consistently lacked one band (16) and showed the consistent presence of 13 common bands. It includes Cagayan, Nueva Vizcaya and Laguna (all ricefields).

Group III consistently lacked three bands (9, 11 and 16) and showed seven consistently present bands (2, 3, 4, 6, 8, 10 and 15). It includes snails from Parañaque, Batangas and Sta. Maria (all grassfields adjoining a ricefield).

TABLE 4. Mean Rf values of the protein fractions in whole body extracts of *Radix quadrasi* from the different collecting areas.

Band no.	Metropolitan Manila					Bulacan		Laguna	Batangas	Cagayan	Nueva Vizcaya	Range of means	Distance variation
	Univ. Philip. Campus, Diliman			San Juan	Para-ñaque	Sta. Maria	San Jose	San Pedro	Nasugbu	Camala-niugan	Bayom-bong		
	CAS[1] pool	Lagoon	NSRC[2]										
1	0.032	0.041	0.034	0.033	–	0.036	0.036	0.026	–	–	0.030	0.026 - 0.041	0.015
2	0.077	0.074	0.067	0.072	0.088	0.073	0.057	0.073	0.069	0.076	0.063	0.057 - 0.088	0.031
3	0.109	0.119	0.108	0.107	0.122	0.109	0.127	0.111	0.112	0.115	0.110	0.107 - 0.127	0.020
4	0.150	0.153	0.150	0.147	0.154	0.152	–	0.151	0.156	0.152	0.153	0.138 - 0.153	0.015
5	0.180	0.186	0.184	0.186	0.187	0.193	0.191	0.194	–	0.204	0.202	0.180 - 0.204	0.024
6	0.243	0.249	0.232	0.247	0.250	0.254	0.245	0.244	0.238	0.257	0.249	0.232 - 0.257	0.025
7	0.335	0.331	0.319	0.328	0.332	0.341	0.341	0.322	0.324	0.323	0.329	0.319 - 0.341	0.022
8	0.407	0.419	0.410	0.416	0.412	0.394	0.392	0.402	0.407	0.414	0.410	0.392 - 0.419	0.027
9	0.463	0.467	0.470	0.468	–	–	0.468	0.483	–	0.498	0.480	0.463 - 0.498	0.036
10	0.565	0.563	0.573	0.538	0.566	0.557	0.578	0.555	0.551	0.573	0.558	0.538 - 0.578	0.040
11	–	0.620	0.610	0.594	–	–	–	0.616	–	0.610	0.620	0.594 - 0.620	0.024
12	–	0.675	0.692	0.692	0.713	0.711	0.679	0.697	–	–	0.671	0.671 - 0.713	0.042
13	0.762	0.750	0.760	0.768	–	0.746	0.729	0.772	0.736	0.735	0.721	0.721 - 0.772	0.051
14	–	0.814	0.822	0.819	–	0.833	–	0.804	0.808	0.822	0.823	0.804 - 0.833	0.029
15	0.876	0.892	0.896	0.897	0.906	0.890	0.897	0.879	0.909	0.900	0.874	0.874 - 0.909	0.035
16	–	0.953	0.975	0.971	–	–	0.970	–	–	–	–	0.953 - 0.971	0.018

[1]College of Arts and Sciences pool, near Pavilion 1.
[2]Natural Science Research Center grassfields.

TABLE 5. Maximum number of whole body extract protein fractions in the different sizes of *Radix quadrasi*, from the different collecting areas, based on 428 snails.

No. of snails/ size class	No. of localities represented	Shell length (mm)	Maximum no. of protein fractions
9	1	6	6
48	9	7	16
44	9	8	16
50	8	9	16
59	11	10	16
48	10	11	16
56	10	12	16
35	10	13	16
24	8	14	16
18	8	15	16
10	6	16	15
5	5	17	16
9	6	18	16
4	3	19	15
5	4	20	16
2	1	21	15
1	1	22	16
1	1	23	7
428			

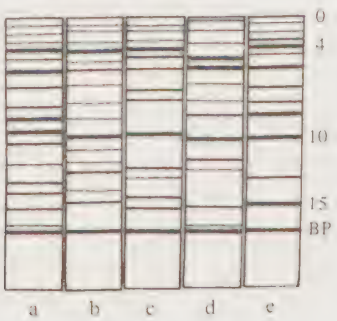

FIG. 2. Schematic diagrams of the protein patterns observed in the whole body extracts of *Radix quadrasi* from the 11 areas. a, Characterized by the presence of all 16 bands and includes snails from the University of the Philippines lagoon, Natural Science Research Center grassfields and the San Juan kangkong field; the snails are oval, semi-oval and oblong. b, Characterized by the consistent lack of one band (16) and shows the consistent presence of 13 common bands; it includes Laguna, Cagayan and Nueva Vizcaya, all ricefields, and the snails are semi-oval and oblong. c, Characterized by the consistent lack of three bands (9, 11 and 16) and shows only seven consistently present bands (2, 3, 4, 6, 8, 10 and 15); it includes snails from Parañaque, Sta. Maria and Batangas, all grassfields near a ricefield, and the snails are oval and oblong. d, Characterized by the consistent absence of three bands (4, 11 and 14) and the presence of 13 bands; the snails are found only in San Jose pond, and their shape is oblong-elongate. e, Characterized by the consistent lack of four bands (11, 12, 14 and 16) and is characteristic of snails from the College of Arts and Sciences pool; the snails are oval and semi-oval.

TABLE 6. Percentage frequency of occurrence of the protein bands in 428 whole body extracts from different sizes of *Radix quadrasi* from the different collecting areas.*

Protein band no.	Shell length (mm)																	
	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
1	100	54	55	66	73	85	82	82	63	67	50	80	33	100	60	100	100	100
2	0	73	52	68	86	89	96	89	88	67	100	100	100	100	100	100	100	0
3	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
4	100	100	98	99	99	99	99	99	99	99	99	99	100	100	100	100	100	100
5	0	88	80	100	95	94	94	91	92	100	70	100	67	100	100	100	100	100
6	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
7	0	71	75	72	73	04	94	91	92	100	70	100	67	100	100	100	100	100
8	0	46	77	82	81	93	98	97	92	94	90	90	100	100	100	100	100	0
9	0	50	68	82	77	90	90	77	58	83	30	40	22	100	50	100	100	0
10	100	75	73	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
11	0	33	41	44	47	46	64	74	58	56	50	60	44	75	80	100	100	0
12	0	69	73	86	81	80	78	69	46	55	30	40	33	75	50	100	100	0
13	0	85	84	90	86	100	100	100	96	100	100	100	89	100	100	100	100	0
14	0	83	68	60	73	76	94	86	67	61	80	60	78	75	80	100	100	0
15	100	100	94	96	100	100	100	100	100	100	100	100	100	100	100	100	100	100
16	0	44	57	44	42	22	62	49	29	28	0	20	22	0	50	0	100	0

*Bands 4, 11 and 14 were absent in San Jose specimens; however, sizes studied were from size 8 mm to 17 mm.

TABLE 7. Protein bands consistently present in whole body extracts of different snails collected from the different areas.

Collecting areas	No. of snails	Sizes represented (mm)	Protein bands consistently present regardless of size	Total no. of bands consistently present in all test runs of all sizes	Maximum no. of protein bands
Diliman					
CAS[1]	43	6-15	1 3 4 6 10 15	6	12
Lagoon	95	7-15	1 2 3 4 5 6 7 11 12 13 14 15 16	13	16
NSRC[2]	54	7-20	1 3 4 5 6 7 8 9 10 12 13 14 15	13	16
San Juan	64	7-22	3 4 5 6 10 11 12 13 14 15	10	16
Parañaque	104	7, 8, 10, 14, 18	3 4 5 6 10 15	6	10
Sta. Maria	16	7-23	3 4 5 6 10 13 15	7	13
San Jose	16	8-17	3 5 6 10 13	5	13
San Pedro	26	7-13, 19	2 3 4 5 6 7 8 9 10 15	10	15
Nasugbu	25	7, 10-12, 14, 16, 18	2 3 4 6 10 13 14 15	8	9
Camalaniugan	38	7-18, 20	2 3 4 5 6 10 15	7	13
Bayombong	41	9-13, 15	3 4 5 6 7 8 9 10 12 13 15	11	15
Total	428				

[1]College of Arts and Sciences pool, near Pavilion 1.

[2]Natural Science Research Center grassfields.

TABLE 8. Protein bands consistently present in *Radix quadrasi* hemolymph from the different collecting areas, based on 109 snails.

Collecting areas	Shell length (mm)	Protein bands consistently present regardless of snail size	Total no. of bands consistently present	Maximum no. of protein bands
Diliman				
CAS[1]	8-10, 11, 15	1 2	4	13 + 6
Lagoon	8, 10-15	2 5 6 7 8	5	16 + 7
NSRC[2]	11-15, 18-19	5 6 7 8	4	15 + 4
San Juan	16, 20-21	3 4 5 6 7 8	6	11 + 3
Parañaque	9-18	6′6[3] 7	2 + 1[3]	8 + 2
Sta. Maria	11-19	1 2 6 7	4	11 + 2
San Jose	10-16	1 2 3 6 7′7[3]	6 + 1[3]	11 + 2
San Pedro	9-16, 12, 14, 16	3 6 7	3	10 + 2
Camalaniugan	8-18, 21	6 7	2	13 + 3
Bayombong	11, 13-15, 18	6′6[3] 7′7[3]	2 + 2[3]	16 + 2

[1]College of Arts and Sciences pool, near Pavilion 1.

[2]Natural Science Research Center grassfields.

[3]Bands number 6 and 7 appeared as one solid band in whole body extracts, but as two very close bands in hemolymph separations from several populations.

Group IV is characterized by the consistent absence of three bands (4, 11 and 14) and the presence of 13 bands. Snails from San Jose belong to this group (natural pond).

Group V consistently lacked four bands (11, 12, 14 and 16) and is characteristic of the snails from the College of Arts and Sciences pool.

On the basis of shell morphology, Group IV, which exhibits a distinctly oblong-elongated shell form possesses morphological features easily identifiable from those of Group I, II, III and V. Electrophoretically, Group IV is shown to exhibit its own characteristic protein pattern, the most conspicuous character being the complete absence of band 4. Band 4 is a dense band that is present in all sizes from all of the other areas studied. The presence of some bands (8 and 9) only in some runs in one size group could be due to the poor quantity of the protein in the said band. The five typical electrophoretic patterns for each of the 11 areas investigated are shown in Fig. 2.

Hemolymph

The same range of Rf values used for the whole body extract was applied to the hemolymph. The results of the hemolymph study of 109 snails ranging from 8 to 21 mm in shell length from the different collecting areas showed 16 protein components. Not all the hemolymph fractions were found in all the sizes and areas studied. Moreover, not all fractions were resolved with equal frequency. Only bands 6 and 7 appeared in all sizes. Some fractions appeared as split bands, although the splitting was not consistent in all the individuals studied. In most cases where splitting occurred, bands 6 and 7 were the ones that were split into two components. These sizes do not correlate with shell size ranges with split band in Table 8. Table 8 is a summary of the protein bands consistently present in the different snail hemolymphs collected from the different areas.

Effect of parasitism

Parasitism was found to affect the protein patterns of the whole body extract of most of

TABLE 9. Percentage frequency of occurrence of whole body extract proteins in uninfected and infected snails from three areas.

Band no.	NSRC[1] grassfield		San Juan		Batangas, Nasugbu	
	Uninfected (54)[2]	Infected (10)	Uninfected (64)	Infected (11)	Uninfected (25)	Infected (13)
1	100	100	61	73	0	27
2	83	20, 80	77	73	100	27
3	100	90	100	100	100	27, 27
4	100	100	100	64	100	27
5	100	100	100	9, 100	0	100
6	100	100	100	55	100	27, 45
7	100	60	75	27, 55	0	0
8	100	60	69	36	64	0
9	100	40	88	9, 64	0	0
10	100	30, 100	100	55	100	18
11	11	40	100	27	0	27
12	100	60	100	64	0	27
13	100	70	100	100	100	78
14	100	70	100	91	100	100
15	100	30	100	91	100	73, 27
16	13	60	78	91	0	0

[1] Natural Science Research Center.

[2] Numbers in parentheses indicate the number of snails electrophoretically examined.

TABLE 10. Mean Rf values of protein bands from whole body extracts of uninfected and infected *Radix quadrasi* from three areas.

Band no.	Natural Science Research Center			San Juan			Batangas, Nasugbu		
	Uninfected	Infected	Additional bands[1]	Uninfected	Infected	Additional bands[1]	Uninfected	Infected	Additional bands[1]
1	0.034	0.034		0.033	0.030			0.042	
2	0.067	0.059	0.087	0.072	0.075		0.069	0.071	0.095
3	0.108	0.116		0.107	0.222		0.112	0.111	
4	0.150	0.146		0.147	0.153		0.156		0.166
5	0.184	0.197		0.186	0.182		0.193		
6	0.232	0.256		0.247	0.226		0.238	0.237	0.278
7	0.319	0.332		0.328	0.338	0.357			
8	0.401	0.431		0.416	0.401		0.407		
9	0.470	0.467		0.468	0.460				
10	0.545	0.537		0.538	0.533	0.591	0.551	0.571	
11	0.610			0.594				0.594	
12	0.692	0.682		0.692	0.678		0.728	0.716	
13	0.760	0.766		0.768	0.761		0.736	0.756	
14	0.822	0.824		0.819	0.811	0.847	0.808	0.817	
15	0.896	0.865		0.897	0.905		0.909	0.927	
16	0.976	0.976		0.971	0.957				

[1]Found in infected snails only.

the infected snails (Tables 9 and 10). Qualitative as well as quantitative differences were noted. Visual inspections revealed the presence of some bands in the uninfected snails which were sometimes absent in the infected ones (e.g., band 8 from Batangas snails) (Table 10). In infected snails, some bands were split into two. Conversely, there were bands from the infected samples that did not appear in the uninfected ones (e.g., band 1 of Batangas snails). There were bands whose frequency of appearance in the infected snails increased over that of the uninfected snails (e.g., band 11 of those from the Natural Science Research Center grassfields). All these are reflected in Table 9.

Table 10 reveals significantschangessin the mobility of some bands as affected by infection. Some moved slower, others faster than their uninfected counterparts. Additional protein fractions whose Rf values did not fall within any of the established Rf ranges also appeared in the infected snails. From the Natural Science Research Center sample, an additional band with an Rf value of 0.087 were resolved between bands 2 and 3 of the uninfected samples. There were three additional bands resolved in the infected samples from San Juan: 0.357 between bands 7 and 8, 0.591 between bands 10 and 11, and 0.847 between bands 14 and 15. The additional bands from Batangas were found between bands 2 and 3 (0.095), between bands 4 and 5 (0.166) and between bands 6 and 7 (0.287). In addition, some of the bands of the infected snails were narrower and stained less intensely compared to its counterpart from the uninfected snails.

DISCUSSION

The present state of taxonomy in many groups of the Lymnaeidae seems to indicate that shell characteristics alone are not an adequate basis for making systematic assessments. Within certain taxonomic segments of the family, there is an apparent high degree of morphological uniformity, although some variations do exist among the individual snails of any population and there is sometimes interpopulational variability. Where shell morphology alone as a basis of identification/classification presents difficulties, electrophoretic analysis may fill gaps of morphological characterization. For example, among the African Planorbidae, Wright & Ross (1965) reported that electrophoretic patterns for different populations of *Bulinus* and *Biomphalaria* were distinctive where no morphological characters previously had been found capable of separating the populations. The present study has shown that morphological variations such as shell color, number of nuclear whorls and relative spire height (both age dependent?), and nature of sutures are not necessarily reflected in the electrophoretic fingerprint of the animals. An exception appears to be the oblong-elongate snails from San Jose.

Electrophoretic analysis of whole body extract samples of *Radix quadrasi* showed that a total of 16 protein components characterize our populations of this species. Individuals 10 mm or more in shell length from all populations had in common bands 3, 6, 10 and 15. Moreover, bands 3 and 6 were consistently found in all sizes from all collecting areas. Band 4, however, was found in all sizes in all areas, with the exception of San Jose, from which the band was completely absent.

The present study shows that the effect of size of the snail on the electrophoretic fingerprint is quantitative rather than qualitative. This is supported by the fact that when the sample load for the larger snails was increased there were no additional bands observed over the original maximum number of bands. Instead, there was only an increase in the density of the bands and in the intensity of staining of some protein fractions. Moreover, bands that appear in snails at size 10 mm shell length or larger were resolved as faint thin bands in smaller snails with increased sample load. Davis & Lindsay (1967) worked on *Helix pomatia* foot muscle extract and showed that size (age) had no qualitative effect on the electrophoretic fingerprint.

Despite variations in the number of distinct protein components in samples of different areas, the species was fully characterized by a pattern clearly recognizable in all areas, namely, the presence of the prominent protein bands 3, 6, 10 and 15 in the whole body extract. All these protein bands were sharply resolved and darkly stained. Except for band 3, all were thick bands. The electrophoretic differences in these areas are characteristic and reproducible. Electrophoretic data using Rf values showsslight differences in the migration characteristics. However, their differences were so slight that the bands initially considered identical based upon visual inspection were indeed the same. In general, geographical distribution of the samples does not appear to bear any relation to the nature of the variation. This seems to occur in a random manner. Of the isolated case (San Jose) which showed a geographic correlation with pattern, no definite explanation is offered from the present study, except that this population possibly may belong to a different species. Balcos (1978) suggested the possibility of a unique protein that depends on the nutritional state of the snails which is affected by environmental conditions. Protein fractions 6 and 7 of the hemolymph were shared by all the samples regardless of size and area, although, as in the whole body extracts, the density and intensity of the staining of some bands varied with size. There were some bands that were thicker and more intensely stained in larger snails than in smaller snails. As previously stated, such differences are quantitative. Hemolymph total protein content varied with size, increasing proportionally from size 8-14 mm and declining slightly at size 15 mm. A similar condition has been reported by Michelson (1966) in *Biomphalaria glabrata*, in which blood proteins increased with increasing size but decreased slightly in larger snails. Hemoglobin, the largest protein component of the hemolymph, was reported by Lee & Cheng (1972) to have a tendency to be in smaller relative amounts in larger snails.

Comparison of the whole body extract and hemolymph protein showed that not all protein fractions recognized in the whole body extract were present in the hemolymph. This was true for most of the fast moving bands, such as bands 9 to 16. In addition, some of the protein fractions present in whole body extract and hemolymph were not of the same amount. Thus, some of the bands were not as thick and as darkly stained as in the whole body extract bands. There were some protein bands in the whole body extract which appeared with a much less frequency in the hemolymph. There were also protein bands in the whole body extract whose corresponding bands in the hemolymph split into two. They were exhibited by bands 1 to 10 (all areas) and occurred with varying frequency. Also, a number of bands distinct in the hemolymph were sometimes either absent, less frequent or less dense in the whole body extract samples. These could be due to technical procedure (e.g., some or most of the hemolymph may have leaked out during protein extraction). Small differences in the dilution technique could have occurred, thus explaining the less frequency of occurrence and less intensity of staining of some bands in the whole body extract. Band 6 was the only protein fraction common to both the whole body extract and hemolymph protein, regardless of size and area.

Definite alterations in the total protein content and protein bands of *Radix quadrasi* resulting from trematode infection have been found in this study. Alterations were in the form of (1) change in the number of resolved bands, (2) decrease in the density of some bands, and (3) change in the electrophoretic mobilities of some bands. Since only naturally infected snails were analyzed, the alterations could not be correlated with the degree and duration of the infection. In other studies (Targett, 1963; Wright & Ross, 1963; Michelson, 1966; Gilbertson et al., 1967; Gress & Cheng, 1973; Michelson & Du Bois, 1975), the number of protein fractions was found to diminish with longer periods of infection. Gilbertson et al. (1967) attributed the effect of parasites on the hemolymph proteins of *Australorbis* (= *Biomphalaria*) *glabratus* to absorption by larval trematodes or reduced synthesis due to altered host metabolism. Reduction or loss of protein bands 7 and 14 in this study seemed to be associated with parasitic infection. This may be taken as evidence of protein loss due to absorption by the parasitic larvae. Gress & Cheng (1973) also postulated that protein utilization by

the parasite could be the cause of hypoprotenemia or reduction in the total protein content. Moreover, there were protein bands in the uninfected snails that showed marked reduction in the intensity of staining or change in the Rf values in the infected ones. Gress & Cheng (1973) attributed this condition to the reduced concentration of these bands. Gilberton et. al. (1967) suggested a qualitative reduction of amino acids by the larval parasites or by the alteration of snail metabolism resulting from reduced synthesis or increased utilization of the amino acids. Protein fractions that were observed in the infected snails, but not resolved in the uninfected ones, have been compared with the cercarial proteins and appeared to be identical with them. These observed changes in the protein patterns of the parasitized snails compared to unparasitized ones also may be immunological. For example, substances produced by the host snail may account for some of the bands resolved only in the infected ones. Immunological reactions of the snails to infection also were reported by Newton (1952) and Pan (1965). The same mechanism possibly can apply to the present studies. As Gress & Cheng (1973) suggested, these additional bands may be reflective of host humoral response. Although it is tempting to conclude that one or several of these might represent new protein fractions which are in some way related to infection, it appears more likely that such bands represent fractions whose Rf values became altered because of reduction in their concentrations (Gress & Cheng, 1973).

The present study showed variation in the maximum number of resolvable bands and variation in the frequency as well as intensity of individual bands in the same or different areas. Moreover, the increase in the number of protein bands in the whole body extract showed a corresponding increase in the hemolymph. These slight variations in the protein patterns occurring in the different areas might be explained by genetic variability within the species. It also can be mentioned that such differences can be used to characterize subspecific taxa with unique characteristics, such as a distinctive relationship to parasitic infection.

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HISTOCHEMISTRY OF THE REPRODUCTIVE TRACTS OF *STAGNICOLA ELODES* (BASOMMATOPHORA: LYMNAEIDAE)

Paul H. Rudolph

ABSTRACT

The female reproductive tract of *Stagnicola elodes* contains 15 types of secretory cells. Some types are found in more than one portion of the tract. The secretions of the cells are primarily polysaccharides, but some contain polysaccharides and proteins and one contains only proteins. The albumen gland contains three types, the posterior convoluted part of the oviduct, one type. The anterior convoluted part of the oviduct is divided into two histochemically distinct regions. Region 1 contains two cell types, Region 2 contains two cell types. The muciparous gland contains three types, the straight part of the oviduct, its caecum and the ciliated groove in the straight part and oöthecal gland contain one cell type. The oöthecal gland is divided into four zones which contain a total of nine cell types. Lipids were present in spermathecal cells.

Each portion of the male tract contains its own complement of cell types which are not shared with other portions. There are 14 secretory cell types in the male tract, of which the sperm duct contains two types, the prostate contains seven types and the penial complex contains five types. The secretions of the sperm duct and prostate are entirely proteins, except for one cell type, which also contains acid mucopolysaccharides. Penial complex cells contain polysaccharides, polysaccharides and proteins, or proteins only.

Comparison with published reports of other lymnaeids shows significant differences in the contents of various portions of the male and female tracts, especially when compared with *Lymnaea stagnalis.*

INTRODUCTION

Histological observations have been made on the reproductive tracts of *Radix auricularia* (Linnaeus) (Eisig, 1869), *R. ovata* (Lamarck) (Klotz, 1889), *R. peregra* (Müller) (Duncan, 1960), *R. natalensis* (Krauss) (Pretorius & van Eeden, 1969) and *Lanx alta* (Tryon) (Baker, 1925). Roszkowski (1926, 1938) compared the histological structure of the prostate of a number of lymnaeids.

Lymnaea stagnalis (Linnaeus) has been the lymnaeid most extensively studied histologically (Holm, 1946; Aubry, 1956; Bournoure & Aubry, 1956; Alaphilippe & Regondaud, 1960). Fantin & Vigo (1968) and Plesch et al. (1971) did histochemical analyses of *L. stagnalis*, the only histochemical works on lymnaeids.

The work presented in this paper is a basic description of the reproductive systems (excluding the ovotestis and hermaphroditic duct) of *Stagnicola elodes* (Say), a common North American lymnaeid snail.

MATERIALS AND METHODS

All snails were laboratory raised as described in Rudolph (1980). They were originally collected from a roadside pond on Liberty Road, 2.2 miles west of Zeeb Road, Ann Arbor, Washtenaw County, Michigan. Voucher specimens from the laboratory populations have been deposited at the Museum of Zoology, University of Michigan (UMMZ). Shell specimens are lot number UMMZ 246000; alcohol specimens are UMMZ 246001.

Reproductive tracts were fixed either in Bouin, Susa or 10% buffered formalin. Paraffin sections were

prepared at 6-8 μm. Formalin fixed, frozen sections were used for lipid determination. Unless otherwise noted, histochemical tests were from Pearse (1968). Histochemical tests performed were: Periodic acid-Schiff (PAS), with and without prior diastase digestion; Periodic acid-paradiamine (PAD); Alcian blue 8GX (pH 1.0)-Alcian yellow (pH 2.5), with and without oxidation and with and without 0.1% aqueous nuclear fast red counterstain (Wendelaar Bonga, 1970, except without HCl hydrolysis); Alcian blue 8GX (pH 1.0)-Ruthenium red (pH 2.5) (Yamada, 1970); Alcian blue 8GX-Critical electrolyte concentration (0.1, 0.2, 0.5, 0.6, 0.8 and 1.0 M $MgCl_2$); Azure A (pH 1.5, 3.5 and 4.0); Azure A (pH 1.5) with prior pepsin digestion; 0.01% Toluidine blue in 30% ethanol; Bromphenol blue; Dimethylaminobenzaldehyde (DMAB); Diazotization coupling; Thiosulphation for protein bound S-H and S-S groups (prostate only, Castino & Bussolati, 1974); Sudan black B (Luna, 1968); Oil red O (Zugibe et al., 1959).

Additional tests, recommended by Grainger & Shillitoe (1952), were performed on the albumen gland only. These consisted of PAS with and without prior pectinase (Sigma Chemical Co.) digestion; 0.2% aqueous toluidine blue; iodine; and ruthenium red.

Other stains used were hematoxylin-eosin and Lillie's allochrome (PAS, methyl blue-picric acid, hematoxylin; Lillie, 1965), with and without inclusion of PAS.

RESULTS

Walter (1969) made a detailed morphological study of *Lymnaea catascopium* Say [= *Stagnicola emarginata serrata* (Haldeman)] which was used as a general guide for *S. elodes*, since no obvious morphological differences were present when I compared the two species. Walter considered *S. elodes* to be the *elodes* "form" of *L. catascopium*. The nomenclature used in the present study is the same as was used previously (Rudolph, 1980). The distribution of the secretory cells in the reproductive systems is shown in Fig. 1. The reactions shown by the secretory cell types are given in Tables 1 and 2.

Female Reproductive System

Albumen gland

The albumen gland consists of numerous tubules, apparently radiating from a central lumen. The lumen is bounded on one side by a ciliated epithelium, which may contain a few secretory cells, and on the other side by the same secretory cells which constitute the rest of the gland. The gland contains three secretory cell types and one non-secretory cell type.

Nearly all of the secretory cells are those which contain galactogen and protein (Type 1). The granules of secretion in these cells are of varying sizes, but all are large. The very small non-secretory cells, identifiable only by their small, triangular-shaped nuclei, are wedged between the apices of the galactogen cells. No cilia could be found associated with the non-secretory cells.

The two remaining secretory cell types are much fewer in number than the galactogen cells. Both are found in the central region of the gland in both layers of cells lining the lumen, in portions of tubules close to the lumen, or in the albumen gland duct before it is free of the gland. They are not present in peripheral portions of the tubules of the gland. Both are difficult to identify since they are so few in number and do not contrast sharply with the galactogen cells.

One of these cell types (Type 2) contains very small protein granules. It is bright pink in sections stained with eosin and is most easily recognized in such sections. The granules of the second of these cell types (Type 3) are larger than those of Type 2 but smaller than those of the galactogen cells. This cell type was recognized first after staining with Alcian blue-Critical electrolyte concentration (0.1 M $MgCl_2$). It is very darkly stained, while the remainder of the gland is faint or unstained. The cells possibly contain protein which contains carbohydrates.

Two points should be mentioned in regard to the contents of the galactogen cells. First, formalin fixation preserves far more PAS-positive material than either Susa or Bouin fixatives.

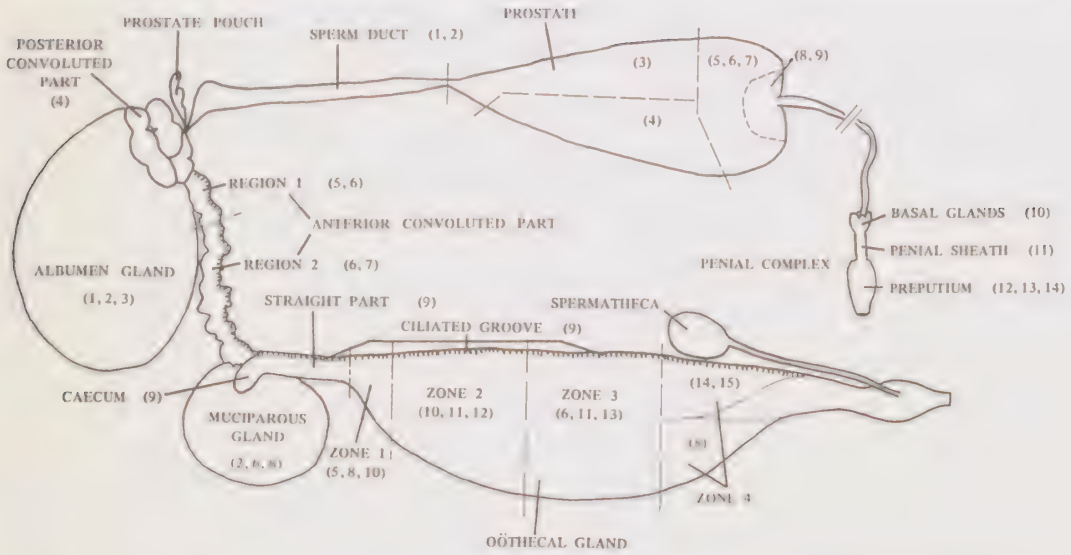

FIG. 1. Reproductive systems of *Stagnicola elodes*. Numbers in parentheses indicate the secretory cell types found in each portion of the reproductive systems.

I believe that the PAS material which is lost using Susa or Bouin is galactogen. Bromphenol blue staining of sections fixed in all three fixatives is of equal intensity, indicating that the protein content is not detectably different. Second, pectinase digestion of galactogen does not remove all PAS-positive material. I believe that at least part of the PAS-positive material remaining after pectinase digestion can be attributed to proteins which contain carbohydrate. The presence of such proteins in the albumen gland of "*Lymnaea palustris*" (= *Stagnicola elodes*) from North America was suggested in an electrophoretic study by Morrill et al. (1964).

The albumen gland duct connects to the remainder of the female tract at the carrefour region. The majority of the cells of the duct are non-secretory, ciliated epithelium, but a few cells contain secretion granules. The contents of these cells were not determined.

The albumen gland duct, hermaphroditic duct, posterior convoluted part of the oviduct and sperm duct unite at the carrefour region. At the entrance of the hermaphroditic duct is the fertilization pocket, which contains no secretory cells but which appears to be weakly ciliated. An oviducal caecum, consisting of a layer of ciliated, non-secretory epithelial cells, is present where the albumen gland duct and the posterior convoluted part of the oviduct meet.

Posterior convoluted part of the oviduct

The posterior convoluted part of the oviduct is a multifolded, disk-like sac, suspended at the carrefour region (see Walter, 1969). It consists of long, thin secretory cells and ciliated cells. I consider all secretory cells of this gland to be of one type (Type 4), which probably contains a mixture of sulphated and non-sulphated mucopolysaccharides. Alcian blue-Alcian yellow staining often is separated into yellow and blue areas. The cells of the portion of the gland into which the eggs must first travel after leaving the oviducal caecum stain more intensely than the rest of the gland with most stains used. This region is probably most concerned with the initial formation of the perivitelline membrane, and the secretion is more highly concentrated in these cells than in the remainder of the gland.

TABLE 1. Staining reactions of the secretory cell types of the female reproductive system of *Stagnicola elodes*.

Stain	Cell type														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Ruthenium red (RR)	R														
Iodine	–														
Toluidine blue, aqueous	β														
Periodic acid-Schiff (PAS)-pectinase	+														
PAS	+++	–	++	+/++	++++	–	++	+/++	++	+++	++/+++	+++	+++	++++	++
PAS-diastase	+++	–	++	+/++	++++	–	++	+/++	++	+++	++/+++	+++	+++	++++	++
Periodic acid-paradiamine	YBr	–	Br	PGr	Br	PGr	YBr	LiT	PBl	P	LiT	RBr	Br	YBr	LiBr
Alcian blue-Alcian yellow (ABAY)	–	–	–	BY-YG	±G	BY-G	Y	Y	BG-YG	G	Y	–	Y	–	$-/Y^{1,4}$
ABRR	–	–	–	BR	–	BR	–	–	B	BR	–	–	–	–	–
AB-Critical electrolyte concentration[2]	0.1 ±	–	0.2 +	0.6 +	0.1 ±	1.0 ++	0.1 +	0.1 +	1.0 ++	0.2 ++	0.1 +	0.1 ±	0.2 +	0.1 ±	$-/0.1^{1}$ $-/++^{1}$
Azure A[3]															
pH 1.5	–	–		++++	–	++++	–	–	+	++++	–	–	–	–	–
Pepsin-pH 1.5	–	–		++++	–	++++	–	–	++++	++++	–	–	–	–	–
pH 3.5	–	–		++++	±	++++	±	+	+++	++++	±	–	++	–	–
pH 4.0	–	–		++++	±	++++	++	++	++++	++++	++	–	+++	–	±
Toluidine blue, alcohol[3]	–	–		γ	±β	γ	β	β	β	γ	β	–	β	–	–
ABAY (oxidation)	YG	GrG		BY-YG	OG	BY-G	Y	Y	BG-YG	DG	LiYG	YG	YG	GrG	BG/G
Bromphenol blue	+++	+++	+++	–	++	–	–	–	++	+	+	+	+	+	++
Dimethylaminobenzaldehyde	++	++		–	+	–	–	–	+++	±	±	+	+	±	++
Diazo-coupling	+++	+++		±	+	±	–	–	+++	+	±	+	+	+	++
Sudan black B	–	–		–	–	–	–	–	–	–	–	–	–	–	–
Oil red O	–	–		–	–	–	–	–	–	–	–	–	–	–	–

[1] For cell type 15, reaction to left of slash is for the homogeneous part of the cell, right of slash for the granules (see text). If no slash is present, no distinction could be made. For other cell types, slash indicates range of strength of reaction.
[2] Molarity of $MgCl_2$ at which staining is observed.
[3] Strength of metachromasia. [4] Stained with Alcian yellow (pH 2.5) only.

Abbreviations: Blue = blue; Bl = black; Br = brown; D = dark; G = green; Gr = gray; Li = light; O = olive; Or = orange; P = purple; R = red; T = tan; V = violet; Y = yellow; – = negative; ± = very weak; + = weak; ++ = moderate; +++ = strong; ++++ = intense; β = purple; γ = red.

TABLE 2. Staining reactions of the secretory cell types of the male reproductive system of *Stagnicola elodes*. See Table 1 for abbreviations and footnotes.

Stain	Cell type													
	Sperm duct		Prostate							Penial complex				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Periodic acid-Schiff (PAS)	+	–	–	–	++	++	–	+	+	+++	+++	++	++	–
PAS-diastase	+	–	–	–	++	++	–	+	+	+++	+++	++	++	–
Periodic acid-paradiamine	Br	–	–	–	Br	Br	–	LiBr	Br	YBr	Br	OrBr	Br	–
Alcian blue-Alcian yellow (ABAY)	–	–	–	–	–	–	–	–	Y-YG	G	G-YG	–	Y-YG	–
AB-Ruthenium red	–	–	–	–	–	–	–	–	–					
AB-Critical electrolyte concentration[2]	–	–	–	–	–	–	–	–	0.2 ++	1.0 ++	0.2 ++	–	0.1 ±	–
Azure A[3]														
pH 1.5	–	–	–	–	–	–	–	–	–	–/±	++++	–	±	–
Pepsin-pH 1.5	–	–	–	–	–	–	–	–	–					
pH 3.5	–	–	–	–	–	–	–	–	–	–/±	++++	–	+	–
pH 4.0	–	–	–	–	–	–	–	–	+	++/+++	++++	–	++	–
ABAY (oxidation)	LiY	Y-YG	LiY	YG	G	LiG	LiG	LiY	B-BG					
Bromphenol blue	+++	+++	+++	+++	+++	++	++	++	++	+++	+	+	–	+
Dimethylaminobenzaldehyde	++	++	++	++	++	+	++	+	+	++	+	±	–	++
Diazo-coupling	++	++	+++	+	+	+	+	+	+	++	+	+	–	++
Thiosulphation			–	±	+++	–	–	–						
Lillie's allochrome	BG	Y-YG	Y	YG	P	P	BG	V	B					
Sudan black B	–	–	–	–	–	–	–	–	–					
Oil red O	–	–	–	–	–	–	–	–	–					

Anterior convoluted part of the oviduct

The anterior convoluted part is a ciliated, convoluted tube which connects between the posterior convoluted part and the muciparous gland and straight part of the oviduct. Running through the anterior convoluted part, straight part and oöthecal gland is the ciliated groove. The anterior convoluted part is divided into two histochemically distinct regions. Region 1 (Fig. 2) connects to the posterior convoluted part and extends a short distance anteriorly. It contains two tall, thin secretory cell types (Types 5 and 6). Most of the cells are Type 5, which have a high polysaccharide and protein content. The polysaccharides are intensely PAS positive and only very weakly acidic. Weak reactivity to Alcian blue-Alcian yellow (without oxidation) can be overlain with nuclear fast red counterstaining. Type 6 cells contain highly sulphated mucopolysaccharides. They are few in number and are scattered throughout Region 1 and Region 2 of the anterior convoluted part, the muciparous gland and part of the oöthecal gland.

Region 2 is more extensive than Region 1 and connects at and wraps partly around the muciparous gland and straight part. Region 2 also contains Type 6 cells scattered throughout the region. The majority of cells are Type 7 and contain acidic mucopolysaccharides.

Muciparous gland

The muciparous gland is located at the juncture of the anterior convoluted part and the straight part of the oviduct, where it opens to the straight part through a short, ciliated duct. The gland is composed of numerous lamellae and contains cell Types 2, 6 and 8 (Fig. 3). Type 8 constitutes most of the cells of the gland and is a large, cuboidal type containing an acidic mucopolysaccharide. The reactions of Type 8 cells are very similar to Type 7 cells, but differ sufficiently to be considered a separate type. PAS reactivity of Type 8 cells is variable from snail to snail, and I was not able to determine the reason for this. I had previously reported (Rudolph, 1976) that in some snails the secretion of these cells showed diastase lability. Further attempts to demonstrate diastase lability have failed and I conclude that these cells do not produce glycogen as a major product.

Type 2 cells are also found in the albumen gland. In the muciparous gland, the main body of the cell is found on the connective tissue side of the lamella. The cell extends to the lumen by way of a thin neck. Type 6 cells are scattered throughout the gland. Ciliation could not be detected in the muciparous gland.

Straight part of the oviduct

The straight part connects with the anterior convoluted part and muciparous gland posteriorly and with the oöthecal gland anteriorly. At the posterior end of the straight part is a caecum, which is tightly appressed to the anterior convoluted part and muciparous gland. The ciliated groove runs through the straight part. The straight part and its caecum are ciliated, but not as heavily as the ciliated groove. The walls of the straight part have inward folds, so that it is not a simple tube in cross section. A single secretory cell type (Type 9) is found in the straight part and its caecum and is associated with the ciliated groove (Fig. 4).

FIG. 2. Junction between Region 1 (dark arrows) and Region 2 (light arrows) of the anterior convoluted part of the oviduct. Stain: Periodic acid-Schiff (PAS). FIG. 3. Muciparous gland. (1) Type 8, (2) Type 6 and (3) Type 2 cells. Stain: Alcian blue-Alcian yellow (ABAY) (without oxidation)-nuclear fast red. FIG. 4. Straight part of the oviduct. Type 9 cells (stained dark). Stain: Diazotization coupling. FIG. 5. Oöthecal gland, Zone 4. (1) Type 8, (2) Type 14 and (3) Type 15 cells. Stain: Methyl blue-picric acid, hematoxylin. FIG. 6. Ciliated groove (arrow) at approximately the middle of the oöthecal gland. Type 9 cells (stained dark). Stain: Diazotization coupling. FIG. 7. Anterior end of prostate. (1) Type 5, (2) Type 6 and (3) Type 7 (unstained) cells. Stain: PAS. FIG. 8. Basal gland of penial sheath (arrow). Stain: ABAY (without oxidation). FIG. 9. Type 11 cells (1) in penial sheath surrounding the penis (2). Stain: ABAY (without oxidation).

2

3
3
2

4

2
1
3
5

6

3
1
1
7

8

2
1
9

The secretions are highly sulphated mucopolysaccharides and proteins. The same cell type is found associated with the ciliated groove in the oöthecal gland, but nowhere else in the female reproductive tract. The straight part cells occasionally may be found within the muciparous gland at the entrance to the straight part, but the change in secretory cell types from Region 2 of the anterior convoluted part and the muciparous gland to the straight part is abrupt and very clear.

Oöthecal gland

The oöthecal gland is a large, elongated portion of the oviduct and is composed of numerous lamellae. I have considered the oöthecal gland to extend from the straight part to the vagina and to include all secretory cells in an anterior direction as part of the oöthecal gland. I consider the vagina to extend from the anterior end of the oöthecal gland to the female gonopore, and have not used the term uterus.

The oöthecal gland is not homogeneous along its length with respect to the types of secretory cells present, but is divided into four general zones which contain a total of nine types of secretory cells. Zone 1 is located at the region where the straight part joins the oöthecal gland and contains cell Types 5, 8 and 10. Types 5 and 8 also extend into the straight part for a short distance. Cell Type 10 is triangular shaped and contains moderately sulphated mucopolysaccharides.

Zone 2 of the oöthecal gland, immediately anterior to Zone 1, contains cell Types 10, 11 and 12. Type 10 cells are more highly concentrated in the longitudinal lamellae, which are located on the ciliated groove side of the gland. Their distribution appears to divide the zone into two parts. Cells of Type 11 are very similar to Type 8 cells and also contain acid mucopolysaccharides. They are darker red after PAS than are Type 8 and are yellow-green rather than yellow after Alcian blue-Alcian yellow (with oxidation). Type 12 cells are broadly triangular, strongly PAS positive and may contain a neutral polysaccharide.

Zone 3, immediately anterior to Zone 2, contains cell Types 6, 12 and 13. Type 12 cells extend through this zone and Type 6 cells are scattered throughout. Type 13 cells are large, cuboidal cells, somewhat similar to Type 11 cells. They are strongly PAS positive and show a moderate reaction to protein stains.

Zone 4, at the most anterior end of the oöthecal gland, connects to the vagina and is divided longitudinally into halves (Fig. 5). The half of the zone opposite the ciliated groove contains Type 8 cells, primarily. Type 6 cells intermingle in the posterior end of this area, but, more anteriorly, Type 8 cells exclusively are present. The portion of the zone on the same side as the ciliated groove, appressed to the prostate, contains cell Types 14 and 15. Type 14 apparently contains a neutral polysaccharide. Type 15 cells contain discrete granules of acid mucopolysaccharides, concentrated at the base of the cells. The remainder of the cell is PAS positive and contains proteins. Anterior to the mixed zone of Types 14 and 15 cells is a region which contains only Type 15 cells.

The tenth type of secretory cell in the oöthecal gland is Type 9 (Fig. 6), found in the ciliated groove throughout its path through the oöthecal gland. Other, non-secretory ciliated cells are present throughout the oöthecal gland.

Vagina, spermathecal duct and spermatheca

The vagina consists of epithelium surrounded by muscular tissue. A thin layer of acid mucopolysaccharides may be found covering the epithelium, and the apices of the epithelial cells stain in the same manner and apparently secrete the covering layer. This material is PAS positive and also stains for proteins.

The spermathecal duct epithelial cells stain the same as those of the vaginal epithelium and contain the same covering. The cells of the spermatheca contain lipid droplets, as shown by Sudan black or Oil red O staining.

Glycogen

Glycogen was demonstrable in ciliated epithelial cells throughout both reproductive tracts. It was especially concentrated in these and other cells in the prostate pouch, spermatheca and muscles of the vas deferens and penial complex in animals isolated prior to processing.

Male Reproductive System

Prostate pouch

The prostate pouch lies in the region of the juncture of the hermaphroditic duct and the female reproductive tract. It is a lateral diverticulum from the sperm duct and is connected to it by a short, ciliated duct. The cells of the prostate pouch are a single layer of non-glandular epithelium. Cilia were not observed in the pouch. At times small, clear, cytoplasmic bulbs were observed at the apices of the cells, indicating a secretory role much as was described for the epithelial cells of the spermatheca (Holm, 1946; Horstmann, 1955).

Sperm duct

The sperm duct connects posteriorly at the bifurcation of the male and female reproductive tracts and anteriorly to the prostate. It is oval in cross section and contains two types of secretory cells intermingled throughout its length. Triangular-shaped ciliated cells are present, appearing to be squeezed between the bases of the secretory cells at the lumen of the duct. The secretory cells are tall cells, with nuclei at the periphery of the cell, and the cells extend to the lumen of the duct via a long extension. Both types of secretory cells contain protein as their secretory product, and are very similar to each other in staining properties. Type 1 cells are weakly PAS positive, while Type 2 cells are negative.

Prostate

The prostate connects posteriorly to the sperm duct via a short, ciliated, non-secretory region, and anteriorly to the vas deferens. The transition between secretory cell types from the sperm duct to the prostate is abrupt. The prostate has a single ventral fold so that the lumen is C-shaped for much of its length, only flattening out at the posterior end where it joins the sperm duct. The secretory cells are arranged into "nests" (Roszkowski, 1926; 1938) in both the prostate and sperm duct, only the "nests" are more easily recognizable in the prostate. The nests are composed of a number of secretory cells surrounded by connective tissue. As in the sperm duct, the secretory cells of the prostate have the nucleus situated at the outer border of the cell and deliver the secretion to the lumen of the gland via a long extension of the cell. Wedge-shaped ciliated cells are present, situated between the bases of the secretory cells.

The prostate contains seven secretory cell types. In the prostate, as well as the sperm duct, Susa fixation was superior to other types used. Also, the cell types were more easily differentiated using Lillie's allochrome than by other techniques. The secretory cells are arranged into general zones, although there is some mixing of cell types between zones.

Type 3 cells begin at the posterior end of the prostate and extend anteriorly, limited to the left side of the gland. Their secretion granules are proteins and stain yellow with Lillie's allochrome. Type 4 cells are in the posterior part of the prostate, beginning just anterior to the junction with the sperm duct. They are located on the right half of the prostate. The zone of Type 4 cells extends more anteriorly than does the zone of Type 3 cells. Type 4 cells contain protein and are yellow-green with Lillie's allochrome.

Types 5, 6 and 7 cells form a general zone anterior to the Types 3 and 4 zones (Fig. 7). Type 5 cells contain protein, possibly glycoproteins, and are purple with Lillie's allochrome. Type 6 cells contain proteins and are purple with Lillie's allochrome. Their granules are larger than those of Type 5 cells and are not stained with thiosulphation for S-S and S-H

groups, while Type 5 cells are intensely stained. Type 7 cells contain very small granules and the nucleus and major part of these cells appear to form a layer around the Type 5 and Type 6 cells. They are green with Lillie's allochrome.

Anterior to the zone of Types 5-7 cells is a zone containing Types 8 and 9 cells. They form a zone surrounding the exit to the vas deferens. The two cell types are intermingled. Neither cell type is very numerous, but Type 9 is more numerous than Type 8. Type 8 cells probably contain glycoproteins. They are PAS positive and are violet with Lillie's allochrome. Type 9 cells contain small granules which are composed of slightly sulphated acidic mucopolysaccharides and proteins.

Penial complex

The penial complex is connected to the prostate by the vas deferens. The vas deferens is non-glandular, consisting of a lumen, ciliated epithelium and layers of circular and longitudinal muscles.

The basal glands of the penial sheath (terminology of Walter, 1969; = proximal chambers of Hubendick, 1951), situated at the junction of the penial sheath and vas deferens, are composed of secretory cells surrounding a lumen which is continuous with the lumen of the penial sheath (Fig. 8). The gland cells line the lumen of each basal gland and continue anteriorly on the inner side of the sheath for a short distance. The secretory cells of the basal glands are of one type (Type 10), which secrete highly sulphated mucopolysaccharides and proteins.

The penial sheath surrounds the penis and connects to the preputium anteriorly. The penial sheath contains one secretory cell type (Type 11). These cells are numerous, with the main body of the cell located in the musculature of the sheath and extending to the lumen surrounding the penis (Fig. 9). The penial sheath cells also are present at the preputium and penial sheath. Type 11 cells contain a slightly sulphated acidic mucopolysaccharide.

The preputium contains three secretory cell types (Types 12, 13 and 14), mainly concentrated in the epithelial lining of the lumen. Type 12 cells are the major type of secretory cells and possibly contain a neutral polysaccharide or a glycoprotein. Type 13 cells are not numerous and are scattered widely among the Type 12 cells. Cells with similar staining properties to Type 13 cells are found in the musculature of the preputium, extending into the lumen via a long extension. Type 13 cells apparently contain acid mucopolysaccharides. Type 14 cells are not numerous, are very small, and contain proteins.

DISCUSSION

It has long been recognized that the reproductive tracts of the Limnophila (the "higher limnic Basommatophora") are highly glandular. It is also well established that the secretions of the female tract are predominately polysaccharides and those of the male tract proteins (see Duncan, 1975, for a review of this subject).

Even though the number of lymnaeid species previously studied is very small, a number of significant differences can be seen, especially when *Stagnicola elodes* is compared to *Lymnaea stagnalis*.

Since only *Lymnaea stagnalis* has been characterized histochemically (Fantin & Vigo, 1968; Plesch et al., 1971), histochemical comparisons of *Stagnicola elodes* will be limited. Histological comparisons are given less attention, since some cells may be similar histologically but not histochemically.

Albumen gland

In *Stagnicola elodes*, three secretory cell types were found in the albumen gland. The majority of cells are of one type, which presumably contain galactogen and proteins. Galactogen

has been found to be present in the albumen gland of every pulmonate thus far studied, so this finding was not unexpected.

The other two secretory cell types have not been reported from the albumen glands of lymnaeids. Reasons for this may be either that they are not present in the albumen glands of those lymnaeids studied thus far or that they have been overlooked due to the difficulty in identifying them.

I have identified a cell which corresponds to one of the other two types (Type 2, a protein-containing cell) in hematoxylin-eosin stained sections of the albumen glands of *Pseudosuccinea columella* (Say) and *Radix auricularia*, but not in *Fossaria* sp. Pretorius & van Eeden (1969) reported a goblet-shaped cell in the albumen gland duct of *R. natalensis*, which may correspond to the Type 3 cell found in *Stagnicola elodes*.

A small, non-secretory cell found in *Stagnicola elodes* albumen gland has been reported in other freshwater snails (e.g., Slugocka, 1913; Pan, 1958; Jong-Brink, 1969; Oberholzer & van Eeden, 1969). Only Holm (1946) mentioned a similar type of cell in lymnaeids (*Lymnaea stagnalis appressa*).

Posterior convoluted part of the oviduct

Plesch et al. (1971) described two secretory cell types in the posterior convoluted part of *Lymnaea stagnalis*, based on differences in toluidine blue metachromasia. I have not been able to show this difference in *Stagnicola elodes* and I consider all secretory cells of the posterior convoluted part to be of one type. This is a conservative interpretation on my part, and it should be noted that the cells at the initial part of the posterior convoluted part, at the outlet of the oviducal caecum, were more intensely stained with many techniques than was the remainder of the gland.

Anterior convoluted part of the oviduct

The anterior convoluted part of *Stagnicola elodes* is divided into two histochemically distinct regions. Region 1 is not present in *Lymnaea stagnalis*. Region 2 corresponds well with the entire anterior convoluted part of *L. stagnalis* (Plesch et al., 1971). Although these authors found three cell types in the anterior convoluted part of *L. stagnalis*, two of them were very similar to each other.

Muciparous gland

The muciparous gland of *Stagnicola elodes* contains three secretory cell types. This contrasts with two found in *Lymnaea stagnalis* (Fantin & Vigo, 1968; Plesch et al., 1971) and (probably) *Radix natalensis* (Pretorius & van Eeden, 1969).

Cell types 6 and 8 of *Stagnicola elodes* are similar to the two types in the muciparous gland of *Lymnaea stagnalis*. The third type in *S. elodes* (Type 2) is also found in its albumen gland. Although it is possible that this cell type could have been overlooked in the albumen glands of other species, it is doubtful that it could have been overlooked in the muciparous gland, since it is clearly differentiable in this gland. Also, it is not present in the muciparous gland of *Pseudosuccinea columella* or *Radix auricularia*, even though present in the albumen glands of those species, nor is it present in the muciparous gland of *Fossaria* sp. (unpubl. observ.).

The straight part and muciparous gland are not connected by a duct in *Lymnaea stagnalis* (Holm, 1946; Fantin & Vigo, 1968; Plesch et al., 1971), *Radix natalensis* (Pretorius & van Eeden, 1969) or *R. peregra* (Duncan, 1960). Similarities to the histology of the anterior convoluted part and the absence of a connecting duct have led to the suggestion that the muciparous gland is an outgrowth of the anterior convoluted part (Duncan, 1960; Plesch et al., 1971). Except for the presence of a short, ciliated duct and a cell type not present in the anterior convoluted part, the same would appear to apply to *Stagnicola elodes*, since the

majority of cells of the muciparous gland and Region 2 of the anterior convoluted part are similar histochemically.

Straight part of the oviduct

The straight part differs considerably from that of *Lymnaea stagnalis*. The secretory cells of the straight part, the caecum from the straight part and those secretory cells associated with the ciliated groove in the straight part and oöthecal gland of *Stagnicola elodes* are all of one type. This cell type corresponds only to the type found associated with the ciliated groove in the straight part of *L. stagnalis*. This cell type apparently is not present in the ciliated groove of the oöthecal gland of *L. stagnalis*. Thus the majority of cells in the straight part of *L. stagnalis* are the same (except the ciliated groove) as those found in its muciparous gland and anterior convoluted part (Plesch et al., 1971). Of other species studied, only *Lanx* (Baker, 1925) appears to have different cell types in the straight part and muciparous gland. In *S. elodes*, the straight part contains a completely different type from its muciparous gland and anterior convoluted part, yet this cell type corresponds to the cells found associated only with the ciliated groove of *L. stagnalis*. Other snails examined apparently are histologically similar to *L. stagnalis*, since no mention is made of the distinctive Type 9 cells that are found in the straight part of *S. elodes*.

Oöthecal gland

The oöthecal gland is a complex structure in regard to the types of secretion present. In *Lymnaea stagnalis* (Plesch et al., 1971), the oöthecal gland is divided into three general zones, compared to four zones in *Stagnicola elodes*. In *S. elodes*, 10 secretory cell types are present, four of which are present in other portions of the female tract. In *L. stagnalis*, seven secretory cell types are present, three of which are present in other portions of its female tract. There is reasonable correspondence between four types of secretory cells in the oöthecal glands of *L. stagnalis* and *S. elodes*.

With the terminology I have used, the uterine secretory cells of Plesch et al. (1971) in *Lymnaea stagnalis* would be included in the third zone of its oöthecal gland, and also are found intermingled with other cells of that zone. Type 15 cells of Zone 4 of *S. elodes* are similar in content and have the same type of distribution as do the uterine secretory cells of *L. stagnalis*.

In addition, the ciliated groove of *Stagnicola elodes* contains secretory cells throughout its length in the oöthecal gland, while that of *Lymnaea stagnalis* does not. It appears that the oöthecal gland of *S. elodes* is more complex than that of *L. stagnalis*.

Prostate pouch

No other lymnaeid studied histologically, except *Lanx* (Baker, 1925), possesses a prostate pouch. Baker did not describe its histology.

Sperm duct

The sperm duct of *Stagnicola elodes* contains two secretory cell types. Pretorius & van Eeden (1969) described two types in *Radix natalensis*, while the cells of *R. peregra* (Duncan, 1960) apparently are all the same type. However, the male tract in *Radix* is not divided into a sperm duct and prostate, so comparisons between the non-bulbar region of *Radix* and the sperm duct of *Stagnicola* may not be valid. *Lymnaea stagnalis* contains three cell types (Holm, 1946; Plesch et al., 1971). Histochemical tests by Plesch et al. (1971) showed the probable presence of phospholipoproteins in all three cell types of *L. stagnalis*, based on Sudan black and copper phthalocyanin staining. Sudan black was completely negative in *S. elodes*, as was Oil red O. The sperm duct cells do not appear to contain phospholipoproteins in *S. elodes*, although copper phthalocyanin was not used in my study.

Prostate

The prostate of *Stagnicola elodes*, with a single longitudinal fold, varies greatly from that of *Lymnaea stagnalis*, whose prostate is composed of many folds. This has long been recognized, and the degree of folding of the prostate wall is an important character in the taxonomy of lymnaeids (e.g., see Hubendick, 1951).

Lymnaea stagnalis contains five secretory cell types in the prostate gland and *Stagnicola elodes* contains seven. The secretions of the *S. elodes* prostate are entirely proteinaceous, except for the small group of Type 15 cells at the exit to the vas deferens. *L. stagnalis* secretions are mainly phospholipoproteins, based on staining with Sudan black and copper phthalocyanin. Cells containing neutral fats are also present in *L. stagnalis* (Plesch et al., 1971). No Sudan black staining was observed in *Stagnicola* and copper phthalocyanin was not done. Phospholipoproteins and neutral fats are not indicated in *Stagnicola*.

Duncan (1975) indicated that proteins and amino acids may be the major constituents of pulmonate prostatic secretions. The results observed in this study on the prostatic secretions of *Stagnicola elodes* agree with that statement.

The arrangement of the secretory cells of the prostate into "nests" agrees with the description of *Radix auricularia* (Roszkowski, 1926), *Fossaria truncatula* (Müller) (Roszkowski, 1938) and *Lanx* (Baker, 1925).

Penial complex

Stagnicola elodes contains five secretory cell types in the penial complex, one in the basal glands of the penial sheath, one in the penial sheath itself and three in the preputium. The basal gland cells, which also partly extend anteriorly along the inside of the penial sheath, contain proteins and sulphated mucopolysaccharides. The penial sheath is highly glandular in *S. elodes*, and also contains secretory cells in *Lymnaea viatrix* (Orbigny) (Paraense, 1976). The penial sheaths of *L. stagnalis* (Plesch et al., 1971) and *Radix natalensis* (Pretorius & van Eeden, 1969) are not glandular.

The only detailed histochemical information on the penial complex of other lymnaeids is on *Lymnaea stagnalis* (Plesch et al., 1971). These workers found that the penial complex contained five types of secretory cells, all located in the preputium. However, it should be noted that *L. stagnalis* contains proximal chambers at the posterior end of the penial sheath (Hubendick, 1951) and that Holm (1946) noted that, in *L. stagnalis appressa*, large goblet cells which contained a neutral prosecretion mass were present in this area. The glandular area was externally visible as a knot-like formation (= basal glands) at the point of junction between the penis and vas deferens. Presumably, then, *L. stagnalis* may contain secretory cells in this region which were not described by Plesch et al. (1971).

Of the five secretory cell types in the preputium of *Lymnaea stagnalis*, four secrete acid mucopolysaccharides and one secretes proteins (Plesch et al., 1971). *Stagnicola elodes* contains three cell types in the preputium. One probably secretes a neutral polysaccharide and protein or glycoproteins, one secretes acidic mucopolysaccharides and one secretes protein.

Keeping in mind the problems involved in comparing histochemical descriptions, it appears that, from the comparison of the types and distribution of secretions between *Lymnaea stagnalis* and *Stagnicola elodes*, sufficient differences exist to make further comparisons worthwhile. I consider differences in staining properties much more important than similarities. Most important are regions of the anterior convoluted part, straight part and oöthecal gland, in which clear differences occur between the two species. Other minor differences also occur in the female tract. The female reproductive tracts and penial complex appear to be more valuable for comparative purposes due to their high polysaccharide content. The male tract seems to be of lesser value since histochemical characterization of proteins is less precise than polysaccharide characterization, but the male tract may be of some potential

value also, especially the characteristics of the penial complex. Possibly electrophoretic comparisons of the sperm duct and prostatic secretions would be of more interest than histochemical comparisons.

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EFFECTS OF FOOD ON GROWTH, FECUNDITY AND SURVIVAL OF *INDOPLANORBIS EXUSTUS* (PULMONATA: PLANORBIDAE)[1]

S. Jantataeme, E.S. Upatham and M. Kruatrachue

ABSTRACT

Effects of various types of food on growth, fecundity and survival of *Indoplanorbis exustus* were studied. Of five types of food tested, snails were found to grow and survive best when fed with a combination of lettuce leaves and the diatom *Achnanthes exigua*. Concerning the fecundity potentiality, snails fed with lettuce leaves and *A. exigua* and with lettuce leaves and the blue-green algae *Nostoc muscorum* yielded approximately the same numbers of egg clusters.

INTRODUCTION

In Thailand, the freshwater pulmonate snail *Indoplanorbis exustus* (Deshayes) serves as the intermediate host of *Schistosoma spindale* Montgomery, the blood fluke of water buffaloes and cattle (Harinasuta et al., 1965). They also serve as the first and second intermediate hosts of *Hypodereum conoideum* (Bloch) and *Echinostoma* spp., the intestinal flukes of ducks (Yokogawa et al., 1965) and rats and ducks (Lie, 1963; Bhaibulaya et al., 1964) respectively, which can be transmitted to man.

To study relationships between snails and their parasites, a large number of snails is required. In order to breed snails in large quantity, information on the most suitable type of food and culture methods is essential. In the present report, we report on a laboratory study regarding effects of food on growth, fecundity and survival of *Indoplanorbis exustus*.

MATERIALS AND METHODS

Cultivation of field snails to obtain laboratory-bred offspring

Indoplanorbis exustus snails were collected from suburban areas of Bangkok, Thailand. In the laboratory, 20 field snails were maintained in a round, white plastic container measuring 9 cm in height and 22 cm in diameter. The containers were 2/3 filled with aged, filtered tap water of pH 7.0-7.2, and were provided with two or three pieces of small stream rocks (heated at 160°C for 6 hr and left to cool before using) and moderate aeration (using air stones and pumping air through plastic tubes). The containers were placed on shelves equipped with 40 watt fluorescent lights which were fixed 20-25 cm above the culture containers. The cultures were maintained in an air-conditioned room, at 28°C, with an 8-hr per day cycle of light. The stock snails were fed with lettuce leaves.

Effects of food on growth and fecundity of laboratory-bred snails

Week old snails, 1.2 mm in diameter, were removed from the parents' containers using a small paint brush. Ten snails were then placed into each of the 50 round, white plastic containers measuring 6.5 cm in height and 12 cm in diameter. Ten containers, with a total number of 100 snails, were used for each of the five types of food tested. Altogether, 500 snails were tested in this experiment. The cultures were maintained in the same manner as those described in the section above.

The types of food tested were (1) fresh lettuce leaves, (2) blue-green algae, *Nostoc muscorum*, (3) diatoms, *Achnanthes exigua*, (4) fresh lettuce leaves and *N. muscorum*, and (5) fresh lettuce leaves and *A. exigua*. The amount of each type of food given to each snail container was tabulated in Table 1.

Snail measurements, snail survival rates, and numbers of eggs laid were recorded once a week for a period of 10 weeks. Voucher specimens are in Mahidol University's Museum of Malacology.

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TABLE 1. Types of food and amounts provided to each snail container of each treatment.

Types of food	Amount given to each snail container
Fresh lettuce leaves	one leaf every two days; the remainder of the old leaf was removed
Nostoc muscorum	1 ml of 95% ground *N. muscorum* every two days
Achnanthes exigua	5 ml of 5% suspension of *A. exigua* every two days
Fresh lettuce leaves and *N. muscorum*	one leaf and 1 ml of 95% ground *N. muscorum* every three days
Fresh lettuce leaves and *A. exigua*	one leaf and 5 ml of 5% suspension of *A. exigua* every three days

RESULTS AND DISCUSSION

Cultivation of field snails to obtain laboratory-bred offspring

Seven to 10 days after the introduction of adult snails to the cultures, the snails started to lay eggs on the sides of the containers, on the rocks, or on the lettuce leaves. The eggs were laid in clusters, were yellow-brown in color and oval in shape, and had a maximum diameter of 0.87-0.95 cm. Each egg cluster was surrounded by translucent albuminoid materials and contained 8-30 eggs. Eight to 10 days were required for the snails to develop and emerge from the egg capsules. The newly emerged snails were light brown and translucent, with diameters of 0.9-1.0 mm. It was found that the newly hatched snails should be maintained in the parent cultures for a week or until they reached 1.2-1.5 mm size before they were removed; immediate removal resulted in high mortality.

Effects of various types of food on growth and fecundity of laboratory-bred snails

The effects of various types of food on growth of *Indoplanorbis exustus* are shown in Fig. 1. Snails cultured with *Nostoc muscorum* or with *Achnanthes exigua* alone grew poorly

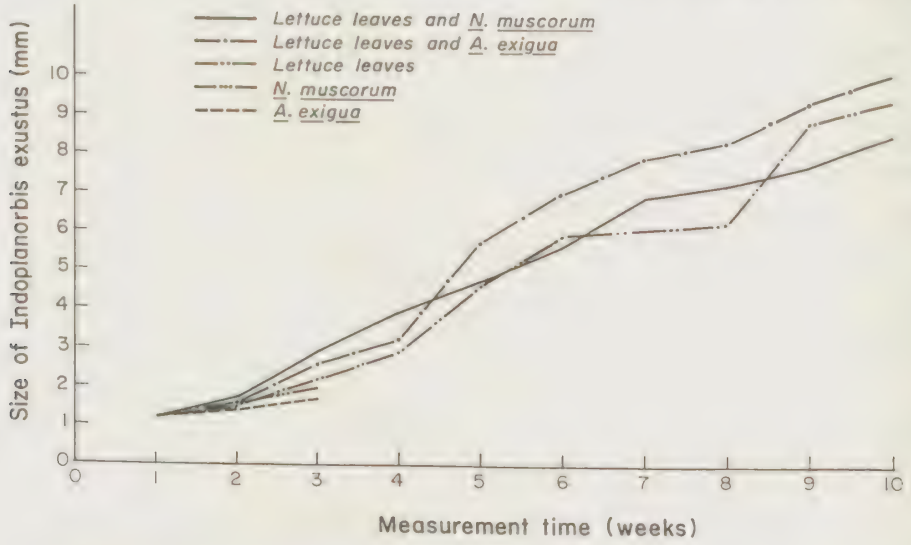

FIG. 1. Laboratory growth of *Indoplanorbis exustus* on different types of food.

TABLE 2. Effects of various types of food on survival, growth and fecundity of *Indoplanorbis exustus*.

Time (weeks)	Types of food														
	Lettuce leaves			*Nostoc muscorum*			*Achnanthes exigua*			Lettuce leaves and *N. muscorum*			Lettuce leaves and *A. exigua*		
	NSS	SS	NEC	NSS	SS	NEC	NSS	SS	NEC	NSS	SS	NEC	NSS	SS	NEC
1	100	1.2	0	100	1.2	0	100	1.2	0	100	1.2	0	100	1.2	0
2	70	1.5	0	62	1.6	0	50	1.2	0	58	1.7	0	94	1.6	0
3	34	2.2	0	10	2.0	0	28	1.7	0	36	2.9	0	94	2.6	0
4	22	2.9	0	0			0			36	3.9	0	80	3.2	0
5	16	4.6	0							36	4.7	0	76	5.7	0
6	12	5.9	0							32	5.6	0	76	7.0	18
7	10	7.1	8							28	6.9	48	76	7.9	36
8	10	7.2	28							28	7.2	62	74	8.3	52
9	6	8.8	12							26	7.7	48	74	9.3	38
10	6	9.3	8							22	8.5	30	74	10.0	40
Total			56			0			0			188			184

NSS = number of snails surviving; SS = size of snails (in mm); NEC = number of egg clusters.

and died at week 3. The mean diameter of the shells in these cultures were 2.0 and 1.7 mm for the *Nostoc* and the *Achnanthes*, respectively. At week 4, snails cultured with lettuce leaves and *N. muscorum* grew best (mean shell diameter = 3.9 mm), followed by those cultured with lettuce leaves and *A. exigua* (3.2 mm) and lettuce leaves alone (2.9 mm). From weeks 4-10, snails cultured with lettuce leaves and *A. exigua* grew best (10 mm), followed by those cultured with lettuce leaves alone (9.3 mm) and lettuce leaves and *N. muscorum* (8.5 mm).

Concerning the fecundity potentiality, snails cultured with lettuce leaves and *Nostoc muscorum* and lettuce leaves and *Achnanthes exigua* produced more egg clusters than those cultured with lettuce leaves alone: 188, 184 and 56, respectively (Table 2). Snails started to lay eggs at week 6, when they reached the size of 6.9 mm.

Regarding the survivorship of snails, it was best in snails cultured with lettuce leaves and *Achnanthes exigua* (74%), followed by those cultured with lettuce leaves and *Nostoc muscorum* (22%) and lettuce leaves alone (6%) (Table 2). Snails cultured with *N. muscorum* or with *A. exigua* alone suffered high mortality and all of them died at week 4.

Therefore, it seems apparent that lettuce leaves are essential for obtaining maximum growth of *Indoplanorbis exustus* under laboratory conditions. However, lettuce leaves alone were not sufficient for the snails because there were high rates of mortality in the containers fed with only lettuce leaves. The addition of *Achnanthes exigua* or *Nostoc muscorum* rendered beneficial effects to snails, which may be due to their nutritional values. Snails fed with lettuce leaves and *A. exigua* survived better and grew faster than those fed with lettuce leaves and *N. muscorum*. Concerning fecundity potentiality, snails fed with either of these latter two types of food yielded approximately the same numbers of egg clusters.

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STONE MICROHABITATS AND THE MOVEMENT AND ACTIVITY OF DESERT SNAILS, *SPHINCTEROCHILA PROPHETARUM*

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ABSTRACT

The pulmonate snail *Sphincterochila prophetarum* is the most abundant snail on rocky hillsides in the Negev and Sinai deserts. A field study on a marked population shows that: 1) the snails select stones in the size range of 200-600 cm^2 as refuge sites for their inactive period; 2) the onset of activity in the snails is determined by rain and soil humidity; 3) the duration of each activity period of *S. prophetarum* is not determined by the amount of rain, but by its distribution over seasonal time; and 4) the snails are active during 5-7% of the time throughout the year, while the remaining 95% of the time the snails are in aestivation under stones.

INTRODUCTION

The Negev ecosystem was described by Noy-Meir (1973, 1974) as "a system regulated by water where input is variable". Westoby (unpubl. data), Bridges, Wilcott, Westoby, Kickert & Wilkin (unpubl. data) and Noy-Meir (1973, 1974) suggested the "pulse-reserve-source" model in order to describe the functioning of desert ecosystems. In this model, reserves are mainly dormant seeds or eggs.

According to the pulse reserve model, the major limiting factor, precipitation, initiates germination or hatching. After such activation, reproduction occurs very rapidly and only a small amount of young snails remain as a reserve in the soil. These last through the dry period and, following further activation, produce a new pulse of biological activity consisting of feeding and reproduction. The life histories of many desert animals appear to conform to this "reserve-pulse" model.

Adaptations of snails and other invertebrates (excluding insects) to certain dry environments are discussed by Billington (1963), Morton (1967), Pomeroy (1967, 1969), Yom-Tov (1970), Schmidt-Nielsen et al. (1971, 1972) and Schachak et al. (1975, 1976). These authors described how different desert snails survive without water and food during long and hot summers and become active during the short, wet periods of the winter season.

We hypothesized that the activity cycles of the desert snail *Sphincterochila prophetarum* (Bourguignat), which lives under stones on the hillsides in both the Negev and Sinai deserts, would conform to the "pulse-reserve-source" model. We studied the mechanisms and activity patterns of *S. prophetarum* which are reported here. The population dynamics of these snails and exploitation of natural resources are reported in previous papers (Steinberger et al., 1981; Steinberger et al., 1982).

MATERIALS AND METHODS

The study area was an exposed, east-facing hillside 500 m above sea level in the central Negev at 34°46′E, 30°50′N. The Negev hills are built of a series of parallel anticlines which are hard Cenomanian limestones and dolomites. Wide loess valleys occur between the anticlines.

On the hill slopes, the dominant shrub is *Zygophyllum dumosum* Boiss. and in the loess plain the dominant shrub is *Hammada scoparia* (Pomel) Iljin. (Danin, 1970). The central Negev highlands have a temperate desert climate, i.e., cool winters and hot summers. The rainfall is low and highly irregular, with

a quotient of variation of 5.0 or more. The rainfall figures for Sde-Boker (average 76 mm, maximum 140 mm, minimum 23 mm, quotient of variation 6.0) are typical of that area.

Due to the very dry air, evaporation values are very high; the anual average evaporation rate according to the Pitche model atmometer (Platt & Griffiths, 1972) is 2600 mm (Friedman, 1971). An important source of moisture in the desert is dew, which falls most heavily from September to November. Up to 37 mm of water from condensation can occur annually, but this figure is deceptive since much of the dew evaporates as soon as the sun rises (Evenari et al., 1971).

Movement and activity of snails was studied on an area of 160 m^2, subdivided into grid units of 2 x 2 m. All the snails found in the 4 x 8 m central area (CA) were individually marked and their location was recorded on a map (Fig. 1). Each snail entering the CA was individually marked, and subsequent observations of snail behavior were made only on the marked snails.

Behavior was recorded during 1-2 h day^{-1}, when the ground was wet (soil moisture was greater than 3%); we observed no activity during the dry periods (soil moisture less than 3%). The following activities were noted: movement in open spaces between stones, feeding on soil algae, mating and laying eggs, movement under stones.

Snails remaining under stones and possessing white epiphragma were classified as dormant (i.e., in aestivation). Initially, 190 observations were made during 1976-1978 on 49 individuals and again later on 31 additional snails entering the area.

In order to examine the relationships between the stone dispersion and snail presence, we measured the projection area (PA) of 71 stones (which provided shelter for 300 snails) by multiplying the maximum horizontal length of each stone by its maximum horizontal width. The vertical height for each stone also was measured.

A Grant multipoint-temperature recorder was programmed to record soil temperature under stones and soil surface each hour during activity and aestivation periods. Two rain gauges provided precipitation data. Voucher specimens have been deposited in the Museum of Zoology, University of Michigan.

RESULTS AND DISCUSSION

Stones as microenvironments

Censusing the different slopes by taking 10 random squares of 10 x 10 m on 27-29 September 1976, we found that the highest population density of *Sphincterochila prophetarum* was on the east-facing slope of the Drorim-geomorphological formation. The highest densities of *S. prophetarum* were found under limestone slabs on this formation (26 snails/100 m^2), an area with a 30-50% stone cover and a soil depth of 100 cm. Most of the stones are between 0-200 cm^2 surface area, and the soil surface is crusted.

The relationship among PA and height of stones, and the number of adult and immature snails, is shown in Fig. 2. Snails of less than 9 mm in diameter were defined as immature because their shells were transparent.

Thirty-six percent of all snails were found under stones with a PA of 400-600 cm^2, and 29% were found under stones with a PA of 200-400 cm^2. Sixty-five percent were found under stones of 5-10 cm thickness and with a depth of 5-10 cm. There were relatively few large, flat stones.

Large stones (PA $>$ 200 cm^2) which are somewhat sunken into the soil provide a deep shelter for snails. Smaller stones (PA $<$ 200 cm^2) apparently are seldom chosen by snails. Only 5% of the stones on the plot (Fig. 3) had a PA of 200-600 cm^2, which probably is one of the factors limiting the dispersion and abundance of *Sphincterochila prophetarum*.

Temperature

In Fig. 4, we summarize temperatures of the soil surface under stones at the end of the activity period and at the beginning of the inactive period. During the activity period, the average maximum soil surface temperature was 27.5°C during the day, dropping to an average minimum of 4°C during the night. Over the same period, comparable temperature under the stones averaged 20.6°C and 4.8°C, respectively. During activity, the soil was moist (soil moisture greater than 3%). Later, when the soil started to dry, snails moved under the stones

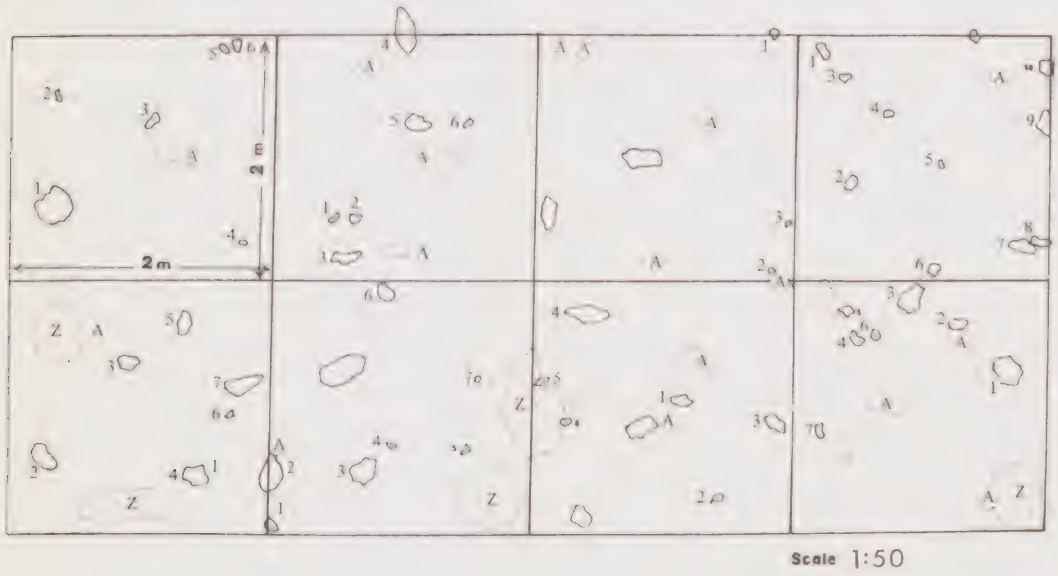

FIG. 1. Map of central area. (A), *Artimisia herba-alba* Asso.; (Z), *Zygophillum dumosum* Boiss.; (5), marked stones.

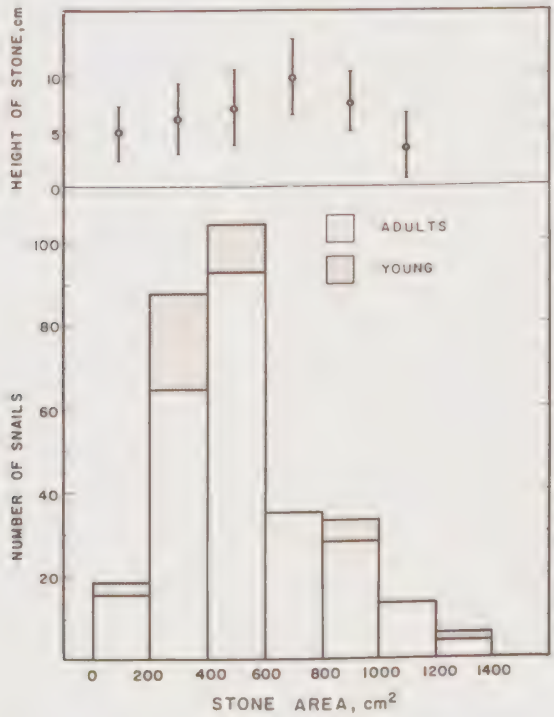

FIG. 2. Relationship between the number of live *Sphincterochila prophetarum* found under stones and the stone sizes.

FIG. 3. Size distribution of stones in the study area.

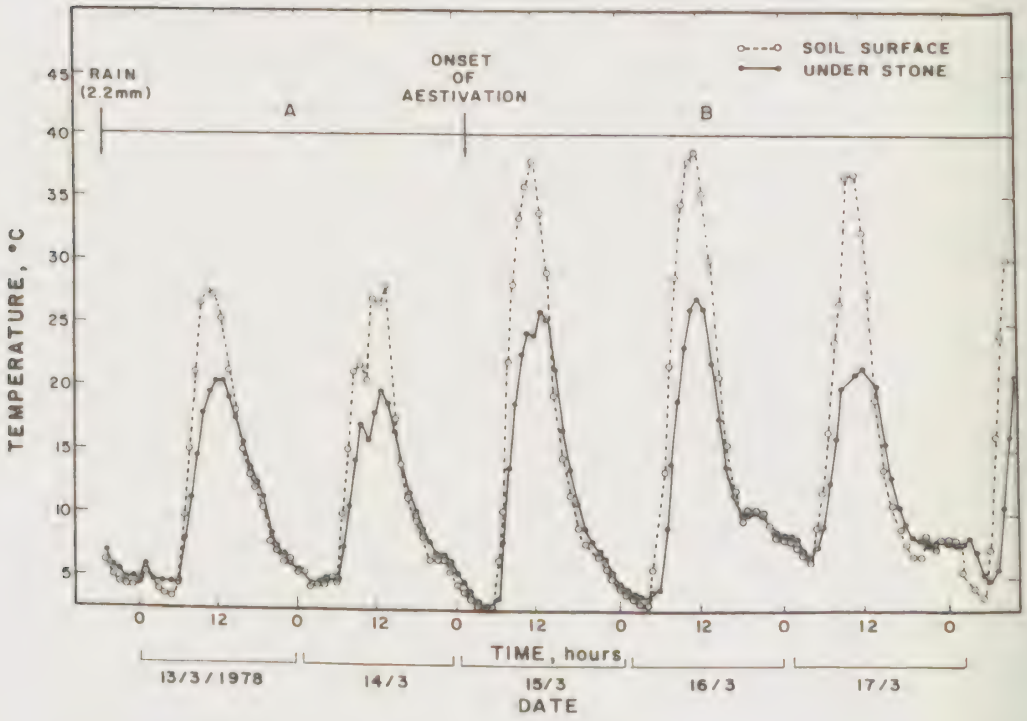

FIG. 4. Temperature fluctuation during the active (A) and inactive (B) period of *Sphincterochila prophetarum*.

and began to aestivate.

During the summer (Fig. 5), the snails remained in aestivation under the stones, where the temperatures were between 41-44°C in the day and 15-18°C at night. The exposed soil surface temperature over the same period of time ranged between 57°C (day) and 11°C (night).

In the four days of activity shown in Fig. 5, the difference between the maximum and minimum soil temperatures was 23-24°C; this increased to 35-39°C in August. The average daily excursion between the maximum and minimum temperatures under the stones was 23.5°C in March, 26°C in July and 27°C in August.

From these data, it appears that the stones reduced the daily temperature fluctuations which would have occurred in their absence. Another potential advantage of stones is to protect the snails from the high incidence of solar radiation.

Types of behavior and individual sequences

Fig. 6 shows the different types of a typical, individual snail's movements from 1976-1978. The behavior pattern started with a feeding stage during the day, followed by movement under the stones. During locomotor activity, the snail's epiphragm was open. Return to the sub-stone microhabitat was followed by another period of surface locomotion (F) feeding, (A) activity without feeding, and (M) mating. Then the snails return to the sub-stone habitat, remaining in winter aestivation until the next rainy season. Similar patterns of activity were recorded in 1977-1978. In 1976-1977, locomotion activity was greater than in 1977-1978, when the snails did not mate.

The movements of a single *Sphincterochila prophetarum* during the entire 1976-1977 activity period are shown in Fig. 7. Nine bouts of activity occurred. At the end of each activity period, the snail moved back under stones. Individual snails use the same stone a number of times, but not necessarily the same stone after each activity period. There was no correlation between rainfall and snail activity. For a total of 27 rain events, snails were active during only 19 of them. However, as shown in Fig. 8, there was a good correlation ($r^2 = 0.79$) between soil moisture and active snails. The snail's activity was discontinued when the soil moisture dropped below 3%.

The annual cycle of *Sphincterochila prophetarum* varies between activity when the soil is moist and inactivity (aestivation) when the soil is dry. During active periods snails are exposed to a hot dry environment, in contrast to the inactive period when the snail is inside the shell, with the opening covered by an epiphragm. Soil moisture greater than 3% permits activity, which can continue for a number of days, during which the snails must store food to complete mating and egg laying. Subsequent feeding results in the storage of organic matter (protein, carbohydrates and lipids) for the long summer aestivation period (Steinberger et al., 1982).

When soil moisture drops below 3%, the snails move under the stones and prepare themselves for the long summer aestivation period by forming an epiphragm. This period may last 200-250 consecutive days in the summer and another 90-140 days in the winter between the activity periods. Thus, *Sphincterochila prophetarum* is active only 5-7% of the days in a year and inactive the remainder of the year.

According to the "pulse-reserve-source" model, activity patterns of *Sphincterochila prophetarum* are similar in some respects to those of annual plants of the Negev. The snails are active only when soil moisture permits, a pattern similar to a seed.

The primary difference between these snails and the seeds of annual plants is the ability of the snails to aestivate after a short activity time. The snails can mate and lay eggs several times in a season, depending on soil moisture levels. If, however, abiotic factors are not favorable, feeding and reproduction will not occur. In contrast, seeds, if they have already germinated, may not complete their life cycle if abiotic factors are unfavorable, and will not have the opportunity to germinate again.

Thus, snails and the annual plants must use different methods to permit continued existence in ecosystems which are regulated by water.

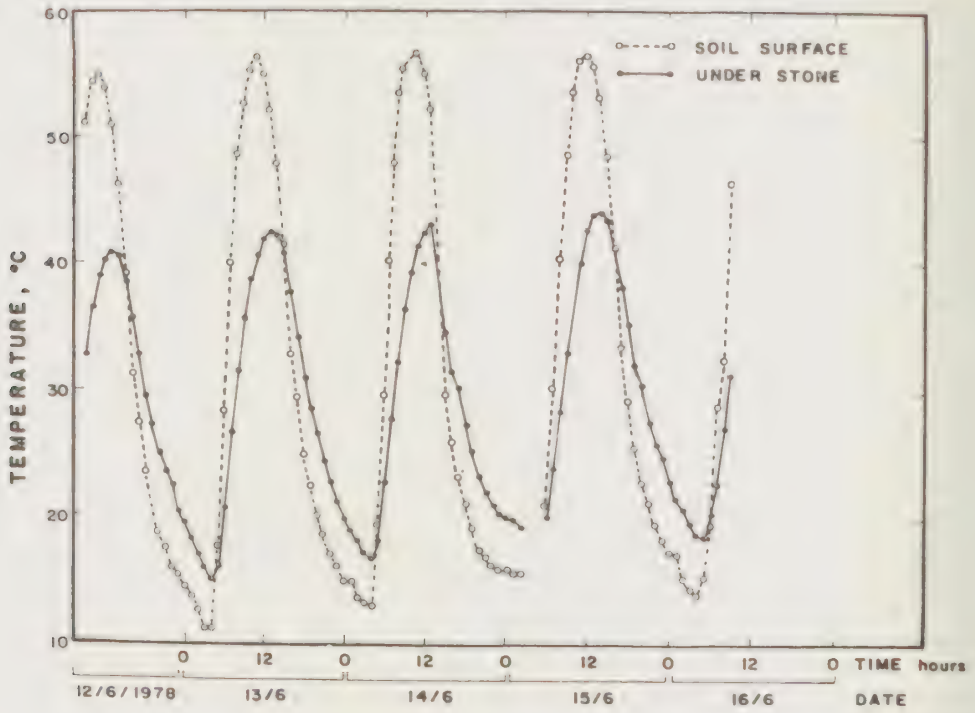

FIG. 5. Temperature fluctuation on soil surface and under stones during the aestivation period of *Sphincterochila prophetarum*.

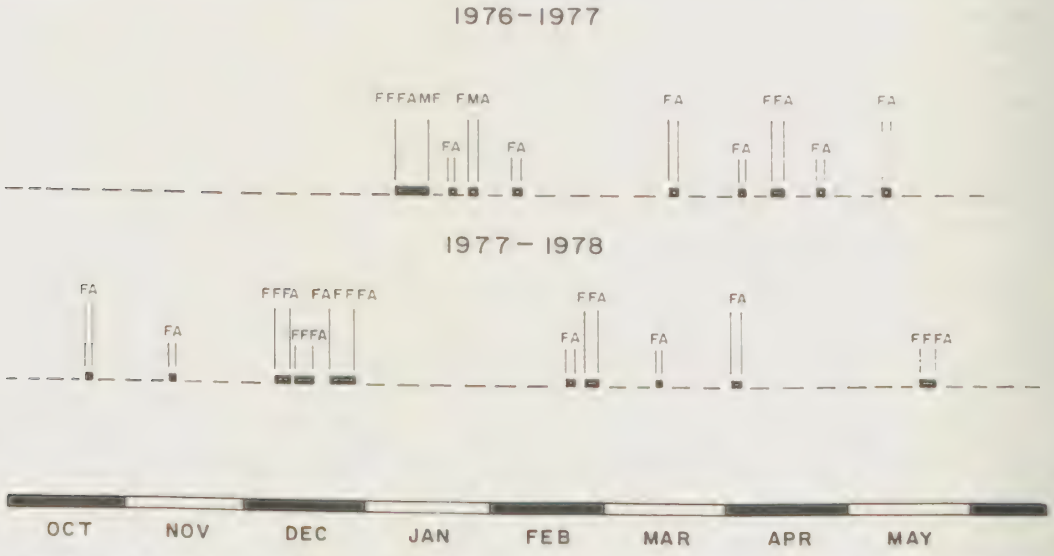

FIG. 6. A periodicity of winter activities and dormancy of *Sphincterochila prophetarum* under field conditions during 1976-1977 and 1977-1978. Each letter above the activity period represents a day.
(---) = Dormancy period; (——) = active period; (F) = feeding; (A) = active and non-feeding; (M) = mating.

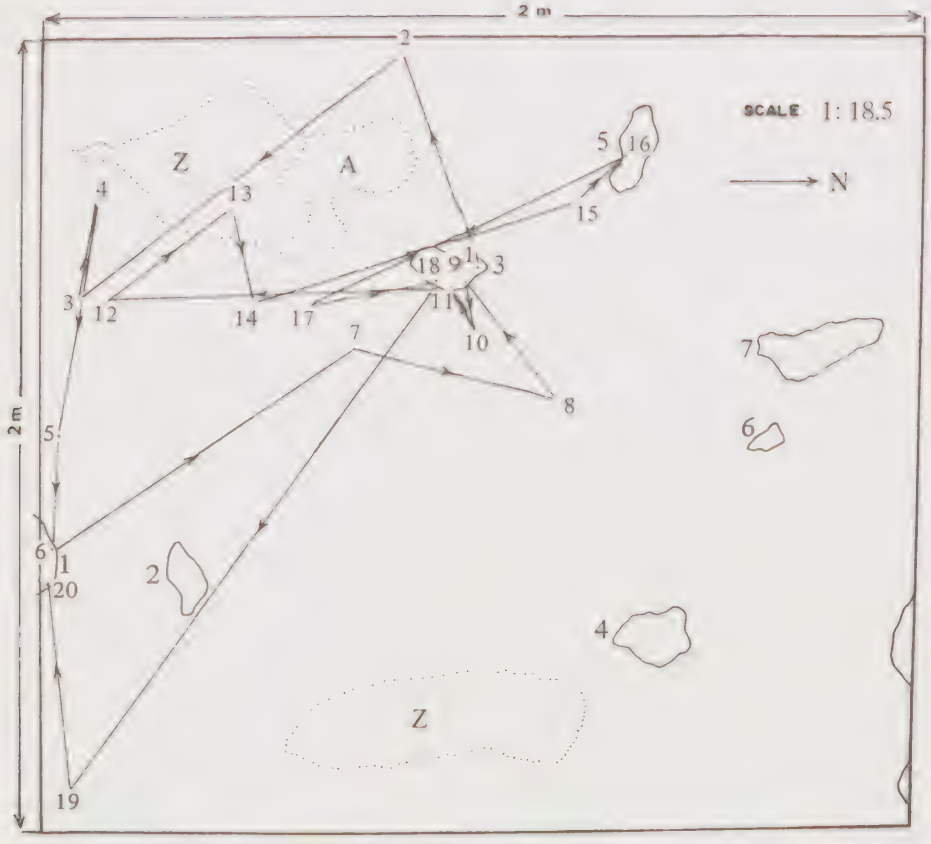

FIG. 7. A typical pattern of movement during the activity period of 1976-1977. The small numbers refer to locations of observation; the large numbers refer to locations of stones in the research area; Z/A refers to plants as in Fig. 2.

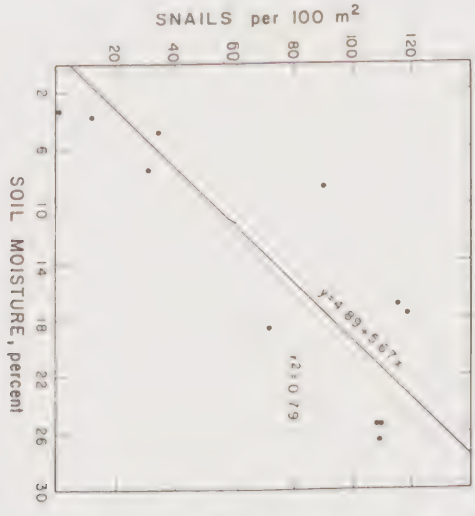

FIG. 8. The relationship between the number of active snails per 100 m² and the percent of soil moisture.

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THE CHROMOSOMES OF EIGHT SPECIES OF THE SUBFAMILY HELICINAE (GASTROPODA, PULMONATA, HELICIDAE) FROM SPAIN

M. T. Aparicio

ABSTRACT

The chromosomes of four species of *Iberus* have been studied, as well as those of *Pseudotachea splendida, Otala lactea, Eobania vermiculata* and *Theba pisana*. Their chromosome numbers range from n=22 to n=30, which is within the range already known in the subfamily Helicinae.

Karyotype relationships indicate that *Pseudotachea, Cepaea* and *Iberus* are closely related genera, as is the case of *Otala lactea* and *Eobania vermiculata*.

These results do not lead to any conclusions about the ancestral karyotype of the subfamily, although some patterns of karyotypic evolution can be postulated.

INTRODUCTION

Twenty-two species of the subfamily Helicinae (family Helicidae) are cytologically known, their haploid numbers ranging from n=22 (*Cepaea nemoralis*) to n=30 (*Theba pisana*) (Patterson, 1969). Most of these species were studied by Perrot (1938a,b,c), and the other results were obtained by Laws (1965), Rainer (1967) and Butot & Kiauta (1970).

On the Iberian Peninsula, the subfamily Helicinae includes eight genera and about thirty species which are not very well known, especially those of the endemic genus *Iberus*. The chromosomes of these snails have not been studied previously. In this paper, we describe the chromosomes of four species of the genus *Iberus*, as well as those of *Pseudotachea splendida, Otala lactea, Eobania vermiculata* and *Theba pisana*, and then discuss the cytotaxonomic aspects which can be derived from our results.

MATERIALS AND METHODS

The eight species under study were collected from 13 localities, whose Universal Transverse Mercator (U.T.M.) grid coordinates are listed in Table 1. Voucher specimens are deposited in the Museo Nacional de Ciencias Naturales, Madrid, Spain. Cytological studies were carried out on the ovotestis germ cells. The specimens found in spermatogenesis were fixed between May and October. The gonads were hypotonized with either deionized H_2O (15 min) or Ohnuki's modified solution (Weber, 1968), then fixed with methanol or ethanol acetic acid (3:1), and finally stained with lacto-propionic orcein and squashed. A minimum of ten cells per specimen were analyzed. Subdivisions of the karyotype were made according to Bantock (1972). In the case of *Iberus gualterianus*, five-day-old embryos reared in the laboratory were squashed *in toto* with a small drop of orcein, thus giving excellent mitoses.

RESULTS

Genus *Iberus*

All four species of the genus *Iberus* studied, namely *I. gualterianus* (Linné), *I. alonensis* (Férussac), *I. marmoratus* (Férussac) and *I. guiraoanus* (Rossmässler), show a very similar karyotype with 44 metacentric and submetacentric chromosomes (Figs. 1, 2, 5, 7). They have a large metacentric pair (A pair) between 12.5 μm and 8.2 μm in size, depending on the species, though we cannot ascertain if these differences were real and have specific value or if they were induced by the technique employed, the stage of coiling observed, etc. The

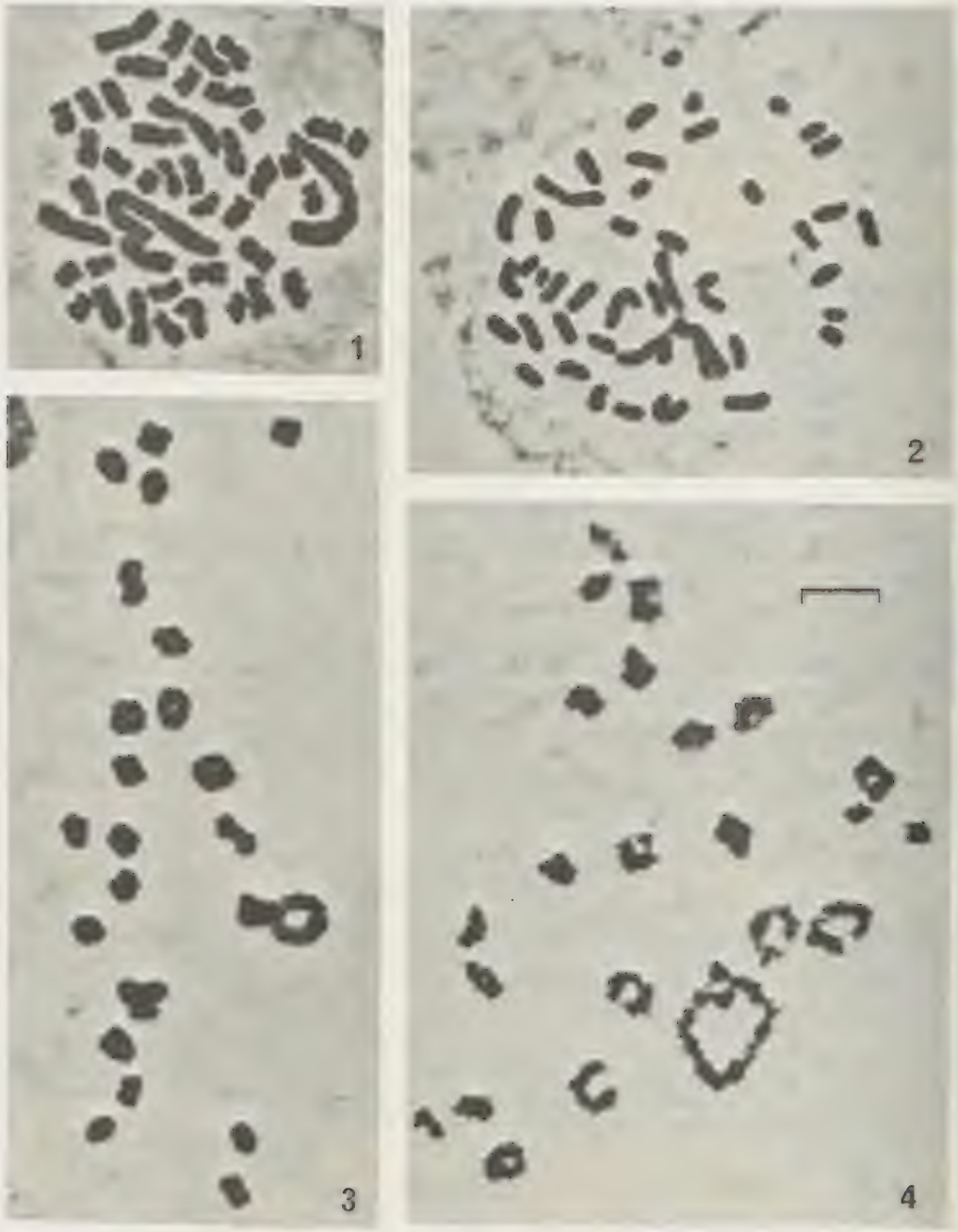

FIG. 1. *Iberus gualterianus*, spermatogonial metaphase, 2n = 44. FIG. 2. *I. alonensis*, spermatogonial metaphase, 2n = 44. FIG. 3. *I. gualterianus*, Metaphase I, n = 22. FIG. 4. *I. alonensis*, diakinesis, n = 22. The bar represents 5 μm.

next large pair (B pair) also is metacentric, being about 4.5 μm in size (3.7-5.2 μm), i.e., about half the size of the A pair. The largest pair of the other chromosomes (C group) is metacentric with an average size of 3.5 μm (3.1-4.2 μm), whereas the smallest pair is between

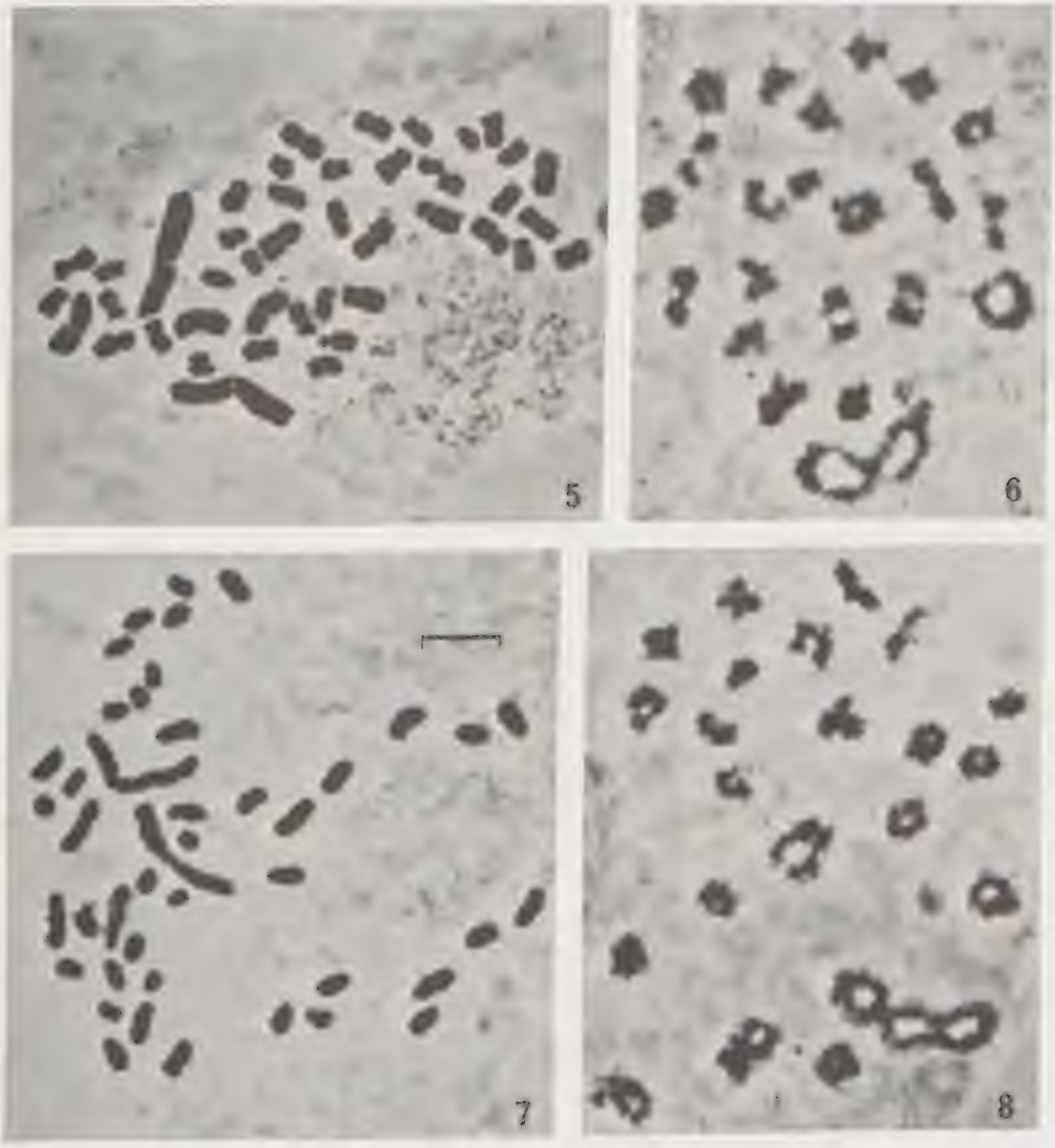

FIG. 5. *Iberus marmoratus*, spermatogonial metaphase, 2n=44. FIG. 6. *I. marmoratus*, diakinesis, n=22. FIG. 7. *I. guiraoanus*, spermatogonial metaphase, 2n=44. FIG. 8. *I. guiraoanus*, diakinesis, n=22. The bar represents 5 μm.

1.2 and 1.7 μm.

In meiosis, a haploid chromosome number of n=22 was observed (Table 1; Figs. 3, 4, 6, 8). During diakinesis, all the bivalents, as a rule, form one chiasma, except for the three largest pairs which form rings. In many cells, the A pair shows three chiasmata. In the case of *Iberus alonensis*, this A pair has a telomeric heteropycnotic region which appears to be associated with the nucleolus, a fact probably related to the localized position of a subterminal chiasma (Fig. 11).

TABLE 1. Chromosome numbers of eight species of the subfamily Helicinae.

Species	n	2n	Localities	No. of individuals
Iberus gualterianus	22	44	Sierra Elvira, Granada 30S VG 3623*	4
Iberus alonensis	22	44	Cabo de Gata, Almeria 30S WF 7366	5
Iberus marmoratus	22	44	Sierra Gorda - Coin, Malaga 30S UF 4761	3
Iberus guiraoanus	22	44	Palles de la Carilarga Cazorla, Jaen 30S WG 1696	5
Pseudotachea splendida	22	44	Foz de Arbayun Salazar, Navarra 30T XN 5028	3
Otala lactea	26	–	Cabo de Gata, Almeria 30S WF 7366	5
			Cabrera, Baleares	
			Alcudia, Mallorca 315-31T EE 1112	
Eobania vermiculata	26	52	Palma de Mallorca 315-31T DD 7877	4
			Santa Ponça, Mallorca 315-31T DD 5575	
			Cabrera, Baleares	
Theba pisana	30	–	Sa Fontseca, Mallorca 315-31T DD 7183	6
			Playa de San Vicente de la Barquera, Santander 30T UP 8906	
			Puerto de Vega, Asturias 30T UP 2917	

*U.T.M. grid coordinate.

Pseudotachea splendida (Draparnaud)

This species has a karyotype very similar to those of *Iberus* spp., with 2n=44, n=22 and the same grouping of the chromosomes (Figs. 9, 10). In addition, the B pair is also about half the size of the A pair.

Otala lactea (Müller)

The haploid chromosome number is n=26 (Fig. 12). The A and B bivalents frequently show two chiasmata, while the bivalents of the C group have only one.

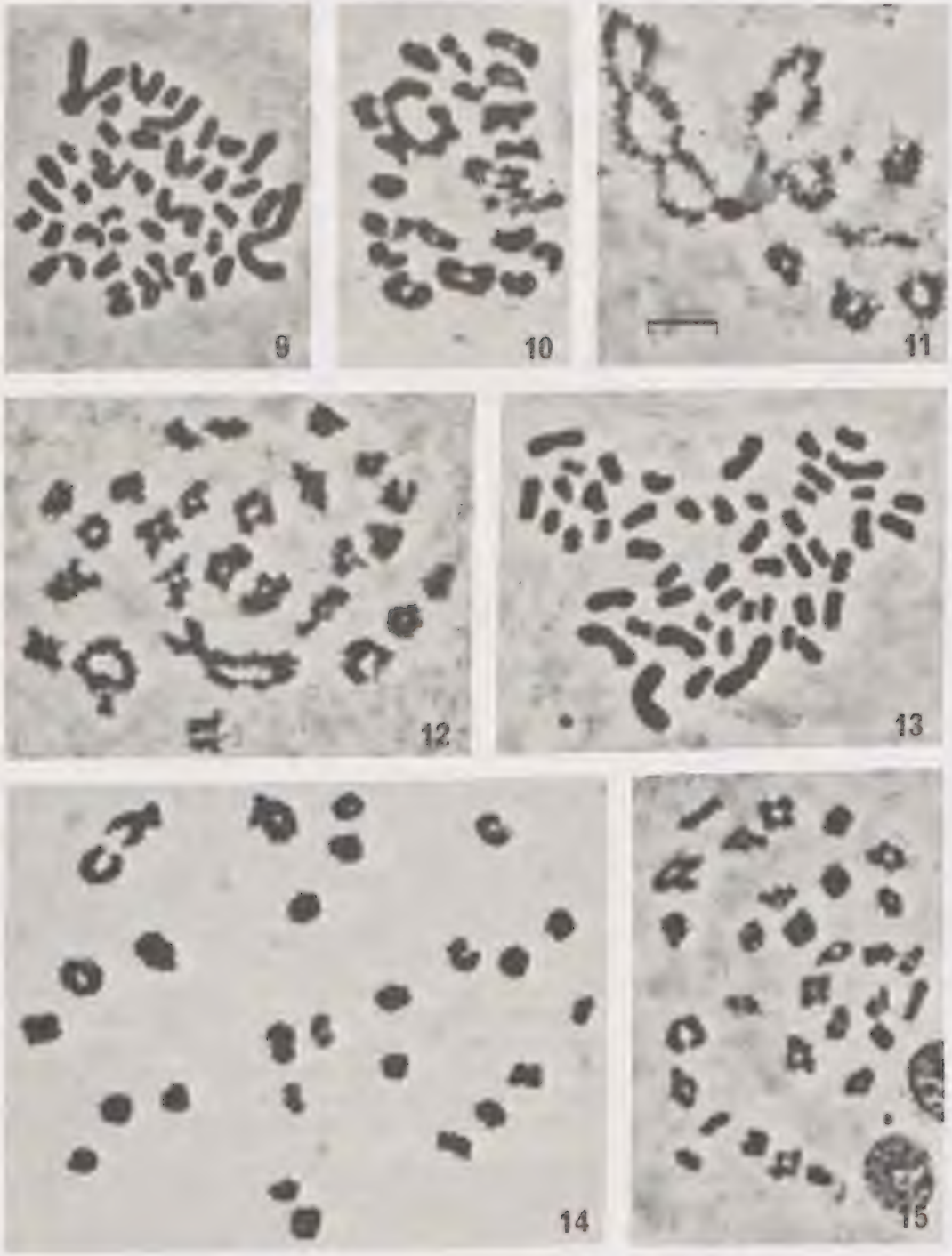

FIG. 9. *Pseudotachea splendida*, spermatogonial metaphase, 2n=44. FIG. 10. *P. splendida*, Metaphase I, n=22. FIG. 11. *Iberus alonensis*, diplotene, the A bivalent showing a nucleolus. FIG. 12. *Otala lactea*, diakinesis, n=26. FIG. 13. *Eobania vermiculata*, spermatogonial metaphase, 2n=52. FIG. 14. *E. vermiculata*, Metaphase I, n=26. FIG. 15. *Theba pisana*, diakinesis, n=30. The bar represents 5 μm.

Eobania vermiculata (Müller)

Spermatogonial metaphases are each made up of 52 metacentric chromosomes (Fig. 13). Chromosome size is rather smaller in this species than in *Otala lactea* (A pair, 5.8 μm; B pair, 4.4 μm; the largest pair of the C group, 3.9 μm; the smallest pair, 1.4 μm).

The haploid chromosome number is n=26. In all diakinesis cells, the A bivalent shows an interstitial clear band (Fig. 14).

Theba pisana (Müller)

Thirty bivalents of relatively small size are observed in diakinesis and first metaphase, decreasing gradually in size (Fig. 15); this fact does not permit an easy subdivision of the karyotype, as in the case of the other species. We have observed one chiasma per bivalent and sometimes two in the largest bivalent.

DISCUSSION

Cytotaxonomic analysis

The haploid chromosome number of the eight species studied ranges from n=22 (*Iberus* spp.) to n=30 (*Theba pisana*). These results are within the range already known in this subfamily (Patterson, 1969).

The species of the genera *Iberus* and *Pseudotachea* form a well-defined group of species with n=22 and very similar chromosome morphology. In all species, there is a large A pair which is twice the length of the next pair (B). This karyotype appears to be very similar to those of *Cepaea nemoralis* (Linnaeus) and *C. hortensis* (Müller) (Perrot, 1938b; Mallett, 1962; Bantock, 1972; Ramos, 1980) and *Pseudotachea litturata* (Pfeiffer) (Perrot, 1938b), which also have 22 pairs of chromosomes, and is not found in the other genera of the subfamily Helicinae (Perrot, 1938b; Rainer, 1967; Butot & Kiauta, 1970; Aparicio, 1981).

Thus, from the cytogenetic point of view, it can be concluded that the genera *Pseudotachea, Cepaea* and *Iberus* are closely related. This is in agreement with the ideas suggested by Schmidt (1855) and Sacchi (1956), who have indicated the existence of a close relationship between the three genera, based on anatomical and conchological grounds respectively, in spite of differences that are sometimes found in shell morphology.

On the other hand, Perrot (1938b) suggested that placing *Pseudotachea litturata* in a different genus from *Cepaea* might not be justified, on account of the karyotypical similarities between these two taxa. However, we think that *Pseudotachea* is well differentiated from *Cepaea* on the basis of morphological characters (for example, in the dart), and that the similar karyotypes (also found in *Iberus*) should be considered only as indicative of an affinity between these three genera, not an argument for grouping them together in the same genus.

Otala lactea and *Eobania vermiculata* are morphologically related species (Germain, 1930) that can be included in a cytogenetic group with the same number (n=26) and similar chromosome morphology. In these species, the length of the B pair is less than half that of the A pair. This fact reinforces the numerical differences that separate this group from the one mentioned above.

Rainer (1967) found n=27 in specimens of *Eobania vermiculata* from Yugoslavia, a number which differs from that of our specimens from Mallorca. As the evidence presented by this author is not very conclusive, it would be interesting to confirm this possible case of numerical polymorphism.

The chromosome number of *Theba pisana* in several Spanish populations (Table 1) appears to be a constant, n=30. This number also was reported by Mallett (1962) in English specimens and by Laws (1965) in specimens introduced into Australia. This number differs from that found in Yugoslavian specimens (n=28) by Rainer (1967).

Karyotypic evolution of the subfamily Helicinae

Contrary to what is found in all the other subfamilies of Helicidae (Aparicio, 1981), the results indicate that a "type" or "modal" number cannot be established for the subfamily Helicinae (Table 2). In contrast, we can distinguish three groups of species according to their chromosome number: one with n=22, another with n=26 or n=27 and the third with n=30.

The origin of these karyotypes is uncertain, as the most probable ancestral karyotype of the group has not yet been determined (Rainer, 1967; Butot & Kiauta, 1969). In addition, as phylogenetic relationships based on morphological grounds have not yet been established, there is not appropriate background against which the cytotaxonomic results can be interpreted.

The fact that the large A pair of chromosomes is progressively smaller in size as the chromosome number increases (or vice versa) suggests that it probably is involved in the numerical changes that have occurred in this subfamily (unless it is polyphyletic). However, we cannot know the direction of the numerical changes, due to the lack of knowledge about the ancestral karyotype.

TABLE 2. Chromosome numbers of the subfamily Helicinae.

n	22	23	24	25	26	27	28	29	30
No. species	8			3	6	7			4

The clear band of the A pair of chromosomes

The clear band observed in *Eobania vermiculata* resembles very closely the ones found in *Cepaea nemoralis* (Price, 1974; Ramos, 1980) and *Helicella itala* (Aparicio, 1981) (the last species belongs to the subfamily Helicellinae (Hygromiidae)). The appearance of this band is variable within and between the species *C. nemoralis* and *H. itala* and has been seen in the four specimens of *Eobania vermiculata* studied. The analysis of a large number of specimens and species belonging to the subfamilies Helicellinae and Helicinae might show whether this character only occurs in some species of the two groups or represents an ancestral condition. In this latter case, the band might have been lost in some species or simply masked by either intrinsic causes (i.e., genetic or physiological) or extrinsic ones (i.e., the methods employed).

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SOME NEW METHODS FOR MORPHOMETRIC ANALYSIS OF GASTROPOD SHELLS

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ABSTRACT

A brief review of approaches to the characterization of shell form is given. Two methods for the quantitative characterization of certain aspects of gastropod shell form are presented. The first provides a measure of the peripheral angle. The second quantifies the contribution of a whorl to shell diameter through the course of shell ontogeny. This contribution is analyzed geometrically into two components: whorl width (suture to periphery of whorl), and angle of descent of the whorl. On a semi-log plot, these data show the deviation of the specimen from gnomonic growth (i.e., growth without change of shape). Both methods are illustrated by analysis of two populations of the land snail *Pleurodonte acuta*.

INTRODUCTION

The shells of gastropods traditionally have been tapped as a rich source of systematic characters. Shells particularly lend themselves to morphometric analyses because of their hardness, which permits precision of measurement, and because of the potentially large amount of taxonomic information they contain.

I describe below two methods for characterization of certain aspects of shell form. The first presents a method for quantifying peripheral angle. The second characterizes the pattern of whorl ontogeny. The contribution of a whorl to shell diameter is analyzed geometrically into whorl width (suture to periphery of a whorl) and the angle of descent of the whorl. The ontogeny of these components is followed in relation to increments of whorl number. Analyses of specimens of the Jamaican land snail *Pleurodonte acuta* (Lamarck) are presented to illustrate these methods. Voucher specimens are in the Florida State Museum (UF 39095 and UF 39096).

BRIEF REVIEW OF CHARACTERIZATION OF GASTROPOD SHELL FORM

Use of simple mensural characters, such as shell length and width, and their ratio, is general in systematic malacology. Other simple morphometric characters such as spire angle also have been employed (e.g., C.B. Adams, quoted in Jacobson & Boss, 1973; Cain, 1977). However, further characterization of form generally involves subjective description of characters such as rate of increase in whorl width (rapid vs. slow), peripheral angle (rounded vs. angular), or the form of the umbilical region (shallow vs. deep).

A more objective approach to characterization of complex shell form has been employed by Gould (Gould, 1969; Gould & Paull, 1977; Gould & Woodruff, 1978). Gould's method involves the measurement of a large number of simple shell features and the analysis of these measurements, or their ratios, by multivariate statistics. This produces a reduced number of characters (factor axes or combinations of original variables) which document the major pattern of variation. This approach is highly empirical, no *a priori* model being assumed.

A more analytical approach to the characterization of shell form, through analysis of the ontogeny of form, was presented long ago by Moseley (1838) and further developed by D'Arcy Thompson (1942) and Raup (1966). They showed that many mollusk shells increase all their linear dimensions in a geometric progression as they grow, thus remaining the same

shape ["gnomonic" growth of D'Arcy Thompson (1942)]. The form of such shells can be characterized by just a few parameters (Raup, 1966). Such an approach has been used in morphometric analyses of *Conus*, which approximate gnomonic growth (Kohn & Riggs, 1975). Recently, Harasewych (1982) has presented a modification of Raup's model, allowing for a more complex generating curve (form of growing edge), including a siphonal canal. However, a great many gastropods do not grow in regular, gnomonic increments and therefore cannot be validly analyzed by such models.

Brown (1911, 1913) developed a rather ingenious ontogenetic characterization applicable to forms with non-gnomonic shell growth. For each successive whorl, he plotted the ordered populations against the mean diameter of each population at the whorl number. His data show that different populations of Jamaican land snails differ in their rates of change in diameter with growth in whorl number. These rates were not constant as in gnomonic growth. Knipper (1939) also used the ontogeny of shell diameter to characterize and compare different land snail populations, but his data were presented as graphs of diameter vs. whorl number plotted together on the same axes. Hubendick (1951) used a similar analysis to compare populations of Lymnaeidae. His method differed in that he made measurements of whorl breadth (i.e., contribution of a *single* whorl to the increase in diameter of the shell) and took measurements every 90°. The second method which I present below further modifies this approach, in order to provide additional information on shell form. Other ontogenetic approaches to the characterization of shell form were presented by Waddington (1929) and Frank & Meyling (1966). Here ratios of shell measurements were plotted as a function of shell diameter.

PERIPHERAL ANGLE

Since the shell surface is curved above and below the periphery in most gastropods, a true peripheral angle, in the geometric sense, does not exist. For a given point on the periphery[1], two more points on the shell surface (one above and one below the periphery) are needed to define an angle. Curved shell surfaces dictate that different choices of points will give different values for peripheral angle. The choice of such points is necessarily arbitrary. They are defined here as being located a certain distance, measured normal to the axis of coiling, inside the periphery. This distance is chosen as a proportion of the diameter of the shell. As discussed here, the method is applicable only to shells with a precisely determinable periphery. *Pleurodonte acuta*, the species used below to illustrate the method, has a periphery clearly and precisely marked by very abrupt curvature of growth lines. Thus, even when the whorls are well rounded, the periphery can be very accurately defined. In certain other taxa where the periphery is not angular or otherwise very precisely marked, color bands might be used to define the location of the periphery and thus give greater accuracy to the method.

Materials and methods

Peripheral angle is calculated here from linear measurements made through an ocular micrometer. An apparatus (Fig. 1) is employed to fit onto a mechanical stage and allow movement of the shell while holding it in a standard orientation (axis of coiling parallel to backward-forward (Y) axis of the stage). This apparatus consists of two pieces of wood screwed together. One piece serves as a base and sits on the microscope stage while attached to the mechanical stage. The other has a modified vernier caliper cemented onto it, but with the jaws free to move. A tack is glued onto each jaw such that the points meet each other as the

[1]The "periphery" is here taken as the part of the whorl most distant from its central axis, or more precisely as the spiral line consisting of all points, each of which represents the point on the outer surface of the shell most distant from the axis of coiling in a radial section (plane passing through axis of coiling).

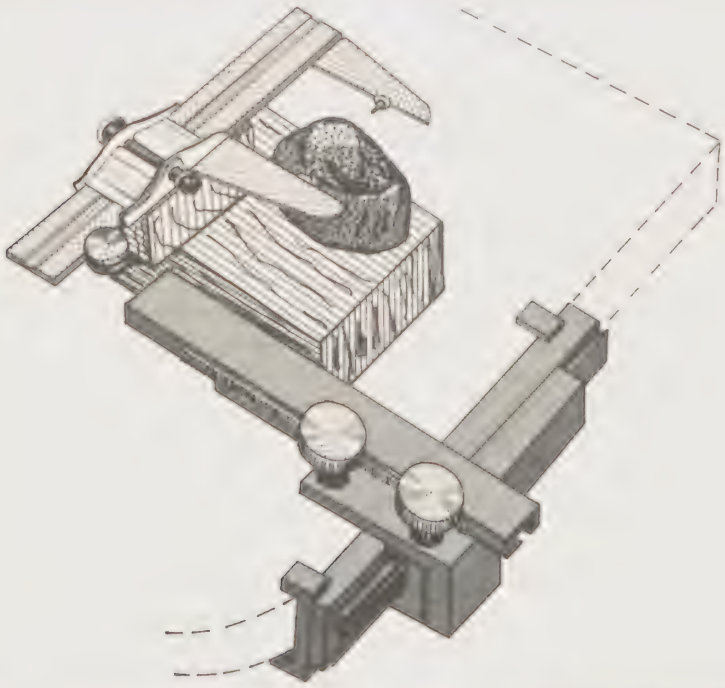

FIG. 1. Apparatus for orienting shell for measurements. See text for description.

caliper is closed. The caliper is oriented such that, when the jaws are opened, the tips of the tacks move apart parallel to the Y axis. The apex and center of the umbilical region of the shell are marked by dots of ink to designate the axis of coiling. The specimen is then placed between the open caliper jaws and the shell orientation and caliper jaw gap adjusted so that the tack points nearly touch the ink dots. The shell is then rotated about its axis of coiling until the point on the periphery at which the angle is to be measured is the same height above the stage as the axis of coiling. The shell is held in place by a piece of clay on the base of the apparatus below the caliper jaws.

The ocular micrometer is cemented onto a cross hair with the micrometer scale parallel to one of the hairs. A mark is made on the ocular such that, when lined up with a mark at the top of the ocular tube, the micrometer scale is exactly parallel to the Y axis of the stage. Marks made on the ocular 90° away from this mark line up the micrometer scale with the X axis. The required measurements are made by 1) orienting the micrometer scale parallel to the X axis, 2) moving the mounted shell parallel to the Y axis until the micrometer axis intersects the shell periphery, 3) moving the shell parallel to the X axis until the center of the cross hairs is a predetermined distance (proportion of diameter, converted to micrometer units, $\overline{AB}$ in Fig. 2) inside the periphery, 4) turning the ocular 90°, and 5) measuring the distances ($\overline{AC}$, $\overline{AD}$) from the center of the cross hairs (A) to the points where the micrometer axis intersects the upper (C) and lower (D) surfaces of the shell. From these measurements, angles θ and ϕ can be calculated as arctan ($\overline{AC}/\overline{AB}$) and arctan ($\overline{AD}/\overline{AB}$) respectively. The sum of these angles is the peripheral angle.

Application to *Pleurodonte acuta*

Adults of two populations of *Pleurodonte acuta* were chosen to illustrate this method. Shells from Culloden, St. Ann Parish, Jamaica, have rounded peripheries, while those from

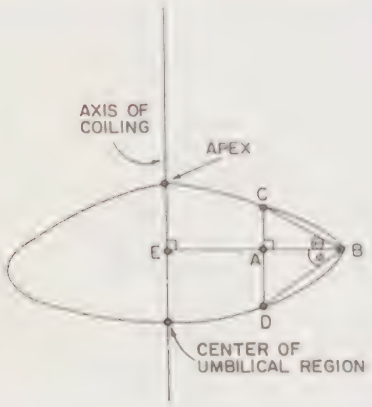

FIG. 2. Profile of lateral view of shell as positioned for measurement of peripheral angle.

Cedar Valley (NE of Cave Valley), St. Ann Parish, have angular peripheries (Fig. 3). Peripheral angle was measured 90° behind the lip of the shell. The length of AB was arbitrarily chosen as 0.05 times the shell diameter. The mean peripheral angle (± S.E.) was found to be 103.4° ± 0.98 for the Culloden sample (n = 21) and 85.0° ± 2.31 for the Cedar Valley sample

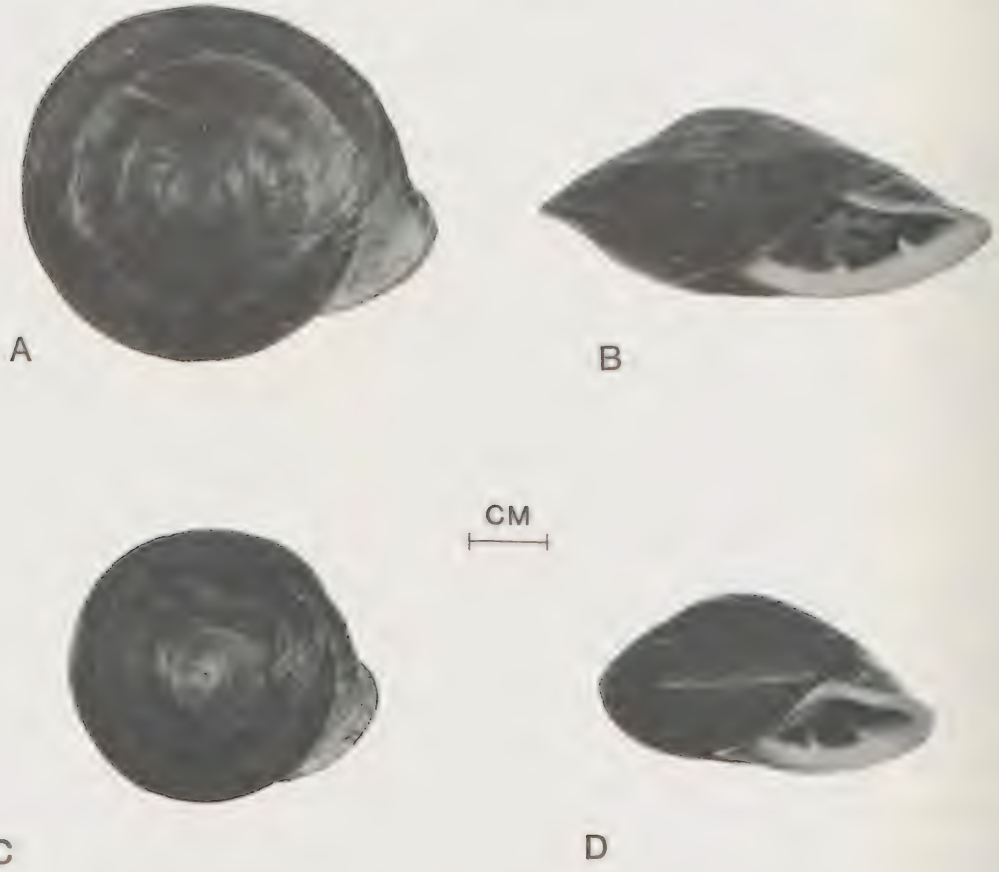

FIG. 3. Shells of *Pleurodonte acuta.* A, B, Cedar Valley, St. Ann, Jamaica. C, D, Culloden, St. Ann, Jamaica.

(n = 21). Thus, the subjectively obvious differences between these populations are matched by equally clear-cut quantitative differences.

A single specimen from Cedar Valley was measured and remounted 10 times in order to determine the repeatability of the method. The range of variation of these estimates of peripheral angle was 3.0°; the standard deviation was 1.4°. In order to assess how much of this error was due to repeatability of the mounted position of the shell vs. measurement error, the same specimen was measured 10 times without remounting it between measurements. The range of estimates was found again to be 3.0°, but the standard deviation was slightly less, 1.1°. The mounting procedure therefore introduces little error. At the magnification used (6.6x), each micrometer unit of $\overline{AC}$ and $\overline{AD}$ contributed 1.0° to 2.9° to the estimated peripheral angle. Thus, the use of a more finely graduated micrometer or higher magnification combined with a longer micrometer scale undoubtedly would reduce the error of measurement.

WHORL ONTOGENY

The contribution of a whorl to shell diameter is a function of two whorl characteristics: the width of the whorl (the linear distance from the suture to the periphery of a whorl) and the angle of descent of the whorl (the angle between the whorl width line segment and the axis of coiling). Formally, it can be seen (Fig. 4) that

$$\overline{FG} = \overline{GH} \sin \beta \qquad (1)$$

where

FG is whorl radius (contribution of whorl to shell diameter),

GH is whorl width, and

β is the angle of descent of the whorl.

Taking the log of both sides we have

$$\log \overline{FG} = \log \overline{GH} + \log \sin \beta. \qquad (2)$$

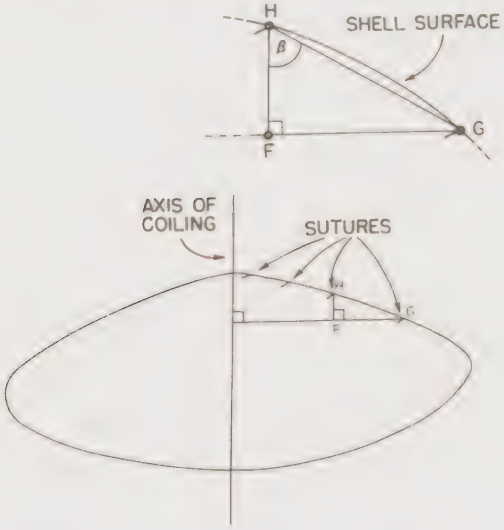

FIG. 4. Profile of lateral view of shell as positioned for measurement of whorl radius, whorl width and angle of descent.

This form is particularly convenient for graphical representation as it allows the contribution of the whorl to the diameter to be expressed as a sum of the relative contributions of whorl width and angle of descent. Determination of these variables at selected whorl intervals provides a characterization of the ontogeny of the whorls.

Materials and methods

The shell is mounted in the apparatus for orientation as described above, with the plane of measurement parallel to the stage. Whorl height ($\overline{FH}$, Fig. 4) is measured along the Y axis. Then the ocular is turned 90° and whorl radius ($\overline{FG}$) is measured. Whorl width ($\overline{GH}$) is calculated as $\sqrt{\overline{FG}^2 + \overline{FH}^2}$, and angle β as arctan $\overline{FG}/\overline{FH}$.

Pleurodonte acuta is particularly well suited for this type of analysis, since the periphery of earlier whorls later becomes the suture of the succeeding whorl. Thus, whorl width is the suture to suture distance in spire whorls. Because of the well-marked periphery (see above), body whorl width (suture to periphery) also is conveniently and accurately determinable. For shells in which the peripheries of whorls are later covered by successive whorls, sectioning of the shells would be necessary to obtain the measurements.

Application to *Pleurodonte acuta*

Whorl characteristics were measured at 180° intervals, starting with the end of the last whorl (directly behind the expanded lip) and working backwards to the first whorl. Before

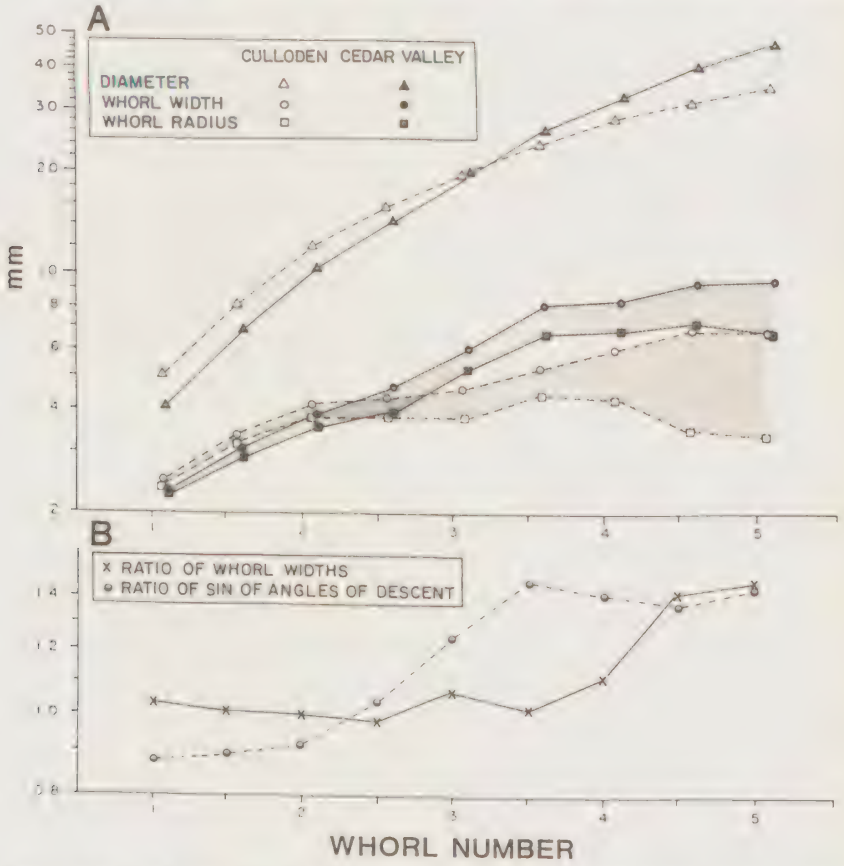

FIG. 5. Comparison of specimens of *Pleurodonte acuta* from Culloden and Cedar Valley. **A**, Ontogeny of diameter, whorl width and whorl radius. **B**, Ontogeny of ratio of Cedar Valley to Culloden specimen with respect to whorl width and sin of angle of descent.

placing a shell in the holder, ink dots were made along the suture and body whorl periphery at 180° intervals to facilitate measurement. Measurements were made at 30x for upper whorls and 6.6x for lower whorls.

While whorl ontogeny measurements have been made on a number of specimens, it is sufficient here to illustrate the method by comparison of a single specimen from each of the two localities previously considered. Fig. 5A presents the results of this analysis. Since whorl characters are plotted on a logarithmic scale, the log of the angle of descent is represented by the difference between the whorl radius and whorl width [log sin β = log (whorl radius) - log (whorl width); see equation (2) above]. Note that log sin β is always non-positive, since sin β is always $\leqslant 1$. Thus, it expresses the proportion by which the angle of descent *decreases* the contribution of whorl width to whorl radius. Comparison of the plots of the two specimens has been facilitated by plotting the differences between them with respect to log (whorl width) and log (sin β) (Fig. 5B). Since these specimens were not measured at exactly the same whorl numbers (the Culloden specimen has slightly more whorls), the values at standard whorl numbers (1, 1.5, 2, etc.) were estimated by linear interpolation, or by extrapolation for points just before the first measurement (Culloden) or just after the last (Cedar Valley).

The angle of descent shows a regular increase with respect to whorl number in both specimens up to whorl 2.5. Beyond that, the angle of descent of the Culloden specimen increases at a greater rate than the Cedar Valley snail, up to whorl 4.5. In the last half whorl, the rates of increase are only slight and more or less comparable. Whorl width of the Culloden specimen is initially larger, but the difference between the specimens decreases at an increasing rate, reaching a maximum at 3.5 whorls and maintaining comparable differences from there to the termination of growth. Whorl width is equal in the two specimens just before whorl 2.5. Diameter (the cumulative sums of the whorl radii) relationships change with development such that the initially smaller Cedar Valley specimen shows a consistently greater rate of increase, reaching the diameter of the Culloden specimen by whorl 3 and continuing to increase in diameter faster up to the termination of growth.

Deviation from gnomonic growth is determined readily from the graph. Such growth would produce straight lines for plots of linear dimensions and a constant value for the angle of descent. Whorl width and whorl radius are seen to increase at a progressively slower rate than under the gnomonic model, while the angle of descent shows a progressive increase. This is the phenomenon that Gould (1969), in a different mathematical formulation, referred to as "doming".

GENERAL DISCUSSION

The morphometric methods described here involve more time than most that have been employed. However, they allow for extraction of a relatively large amount of information in an objective, quantitative manner. These methods allow for more detailed study of museum specimens, which often are the only material available for systematic studies. They are of particular value in the study of fossil material, where only morphological characters are available.

ACKNOWLEDGEMENTS

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BRIEF COMMUNICATIONS

* * * * *

CUBAN ENDEMIC MOLLUSCS INFECTED WITH *ANGIOSTRONGYLUS CANTONENSIS*. – Cuban land snails are extremely abundant, and there is practically no locality in which they are not represented. Due to the insular character of the fauna and the geographical isolation, many snail species and subspecies present in Cuba are highly endemic.

Angiostrongylus cantonensis Chen was first identified in Cuba at the Institute for Tropical Medicine "Pedro Kouri", when it was isolated from the pulmonary artery of rats captured in houses of patients with eosinophilic meningoencephalitis (Aguiar et al., 1981a,b). A large number of land and freshwater molluscs are able to serve as intermediate hosts of this parasite, mainly because of the diversity of conditions in which the nematode larvae can survive (Richards & Merrit, 1967). Marine molluscs have been infected experimentally (Cheng & Burton, 1965), which increases the danger of human infection, since some of these molluscs are used for human consumption and are eaten raw.

The great survival capacity of the larvae enables them to adapt to many different species of mollusks. Thus, this Asian parasite is able to adapt to Cuban endemic molluscs, even though most of the molluscs have an extremely restricted geographic distribution. In 1981, we reported six new intermediate hosts of *Angiostrongylus cantonensis* for Cuba (Aguiar et al., 1981a). The present paper adds to that list.

Cuban endemic land snails were collected in different localities and systematically classified according to pertinent keys and papers (Aguayo & Jaume, 1942; Pérez Farfante, 1942; Jaume & Torre, 1976; Jaume, pers. comm., 1981). Voucher specimens have been deposited in the Museum of Zoology, The University of Michigan.

Using a technique developed in our laboratory, the molluscs were examined to determine whether they did or did not carry second and third stage larvae of *Angiostrongylus cantonensis*. (Our method is easier than the one of Wallace & Rosen (1969).) The steps of our technique are as follows. (1) The molluscs are macerated in 0.85% saline; if the molluscs are very small, they can be crushed with their shells; the largest molluscs must be removed from the shell with forceps. (2) The macerate preparation is left in Gálvez equipment (Gálvez, 1978) for 2 hr. (3) The solution containing the larvae is extracted, and (4) centrifuged for 5 min at 1500 rev/min. (5) The liquid is drained and the sediment analyzed for larvae (second and third instar larvae) with a microscope.

Of the sixteen species of Cuban endemic molluscs examined, 11 were found to have natural infections of *Angiostrongylus cantonensis* (Table 1). All of the infected species represent new records as intermediate hosts of the parasite. Infected snails included not only common species, but highly endemic ones as well (e.g., *Tetrentodon (T.) perdidoensis* and *T. (Scalaricoptis) filiola*, which are strictly limited to a calcareous wall or hillock in Escaleras de Jaruco, Havana Province).

TABLE 1. Cuban molluscs examined for infection with *Angiostrongylus cantonensis*.

Species of molluscs	Infected	Locality
Eutudora jimenoi ("Arango" Pfeiffer)	–	Jaruco
Chondropoma pictum arangoi (Torre & Bartsch)	–	Jaruco
Tetrentodon (Cilindricoptis) sp.	+	Jaruco
Tetrentodon (Tetrentodon) perdidoensis Jaume & Torre	+	Jaruco
Tetrentodon (Scalaricoptis) filiola Jaume & Torre	+	Jaruco
Zachrysia auricoma auricoma (Férussac)	+	Jaruco
Gongylostoma arangiana ("Gundlach" Arango)	–	Jaruco
Ustronia gouldiana (Pfeiffer)	–	Jaruco
Farcimen (Farcimen) tortum (Wood)	+	Jaruco
Helicina adspersa Pfeiffer	+	Jaruco
Rhitidopoma sp.	+	Jaruco
Emoda submarginata (Gray)	–	Jaruco
Emoda sagrayana (d'Orbigny)	+	Soroa
Viana regina (Morelet)	+	Soroa
Jeanneretia bicincta (Menke)	+	Soroa
Polymita picta (Born)	+	Baracoa

We conclude that this parasite, a native of Asia and recently found in our country (possibly imported

in snails on ornamental plants (Jaume et al., 1981), is now widely spread in Cuba and has infected cosmopolitan snails inhabiting Cuba, as well as endemic ones, some of which are limited to very restricted areas. Therefore, a systematic study should be undertaken in order to determine the susceptibility of all Cuban molluscs to infection with *Angiostrongylus cantonensis*, and at the same time to learn the distribution of the parasite in the country, in both snails and rats. This study should be accompanied by the establishment of adequate control measures for the disease.

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GLUTAMATE-OXALOACETATE TRANSAMINASE VARIABILITY IN FOUR POPULATIONS OF *PARAFOSSARULUS MANCHOURICUS* (GASTROPODA: PROSOBRANCHIA). – The bithyniid snail *Parafossarulus manchouricus* (Bourguignat) is the molluscan intermediate host of the Chinese liver fluke *Clonorchis sinensis* (Cobbold) in China, Taiwan, Korea and Japan. Although the liver fluke itself has received considerable attention, the snail hosts have received comparatively little study, especially in regard to their geographic variability. The purpose of this paper is to report on the glutamate-oxaloacetate transaminase (GOT) variability in four populations of *P. manchouricus*.

The snails used in this study were field collected from four different allopatric localities: Chongpyung and Haman, Korea (collected 27 September 1981 and 13 October 1981, respectively, by Mr. J.K. Chang); Taiwan, Republic of China (collected 18 December 1981 by Dr. P.C. Fan); and Kurume, Japan (collected 29 October 1981 by Dr. Ichiro Miyazaki)*. For the electrophoretic studies, 43 individuals were used from the Chongpyung population, 31 from Haman, 25 from Taiwan and 15 from Kurume. All snails were parasite free. They were starved for two days, then their shells were removed and the animals frozen at -70°C until ready to process. In preparation of the samples for electrophoresis, each snail was minced on ice with a scalpel, mixed with 200 μl of distilled water and sonicated with a Biosonic III sonicator for a few seconds. The samples were centrifuged at 5,500 rpm at 4°C for 30 min, after which the supernatant was collected for conventional starch gel electrophoresis. The electrophoretic apparatus and procedures were as described by Kitikoon (1982). A 15% starch gel was prepared using equal amounts of Electrostarch (lot no. 392) and Connaught Starch Hydrolysed (lot no. 168-1). A bromphenol blue marker was used to follow the migration of the buffer, and gels were run until the marker reached the anodal wick (about 9 cm from the origin). Electrophoretic buffers were prepared by the system of Poulik (1957). The glutamate-oxaloacetate transaminase (GOT) electromorphs were resolved in 0.2 M Tris-HCl buffer system, pH 8.0. The substrate, stains and buffer were as follows: α-ketoglutaric acid (100 mg), α-aspartic acid (150 mg), pyridoxal-5-phosphate (5 mg), fast blue BB salt (100 mg), 0.2 M Tris-HCl buffer, pH 8.0 (50 ml).

In all populations except Chongpyung, only single-banded individuals were found (Fig. 1). The band was a fast band, with an Rf value of 0.372. The Chongpyung population had individuals (14) with the same fast band as the other three populations, but some individuals (14) had a slow band (Rf value 0.295). Other individuals (15) had both fast and slow bands, and an intermediate band (Rf 0.333) as well. The GOT bands of five individuals of the Chongpyung population are shown in Fig. 1. Eighteen other individuals of this population are shown in Figs. 2 and 3.

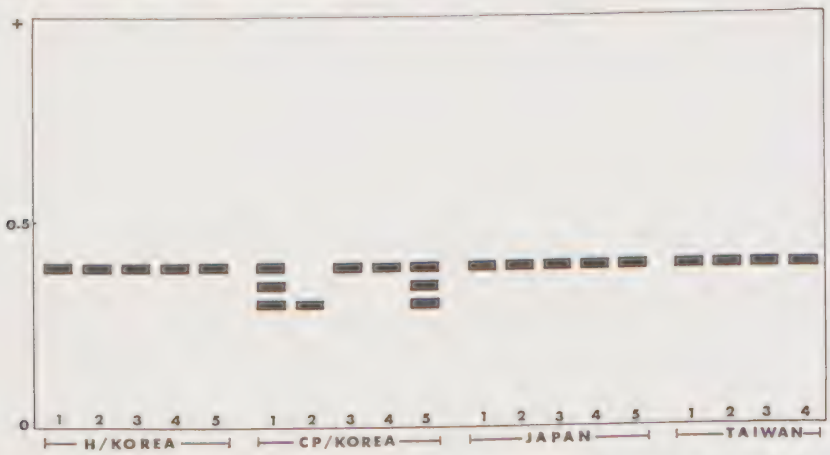

FIG. 1. Comparison of the glutamate-oxaloacetate transaminase allozyme patterns in four populations of *Parafossarulus manchouricus*. Abbreviations, symbols and numbers: H/Korea = Haman (Korea) population; CP/Korea = Chongpyung (Korea) population; O = origin of the gel; + = anodal end of the gel; 0.5 = half-way point between the origin and the front; nos. 1, 2 & 3 = males, and 4 & 5 = females in H/Korea and CP/Korea populations; nos. 1 & 2 = males, and 3, 4 & 5 = females in Japanese population; nos. 1 & 2 = males and 3 & 4 = females in Taiwan population.

The electromorphs of GOT are assumed to be encoded by different alleles at the same genetic locus. On the basis of its banding patterns, GOT is assumed to be a dimer. Heterozygotes were recognized by the possession of an intermediate band, as well as both fast and slow bands. Thus, there is a significant difference in regard to GOT between the two Korean localities.

Also, there may be a significant difference between the populations in regard to transmitting *Clonorchis sinensis*. Haman, in the southern part of Korea, is recognized as one of the highly endemic localities of clonorchiasis. Chongpyung, in the middle part of Korea, is located at the boundary line between low endemic (Goyang Gun, Kyung-Ki Do) and non-endemic (Kangwon Do) areas (Kim, 1974). It would be

*Voucher specimens (UMMZ 250174-250177) are in the Museum of Zoology, University of Michigan.

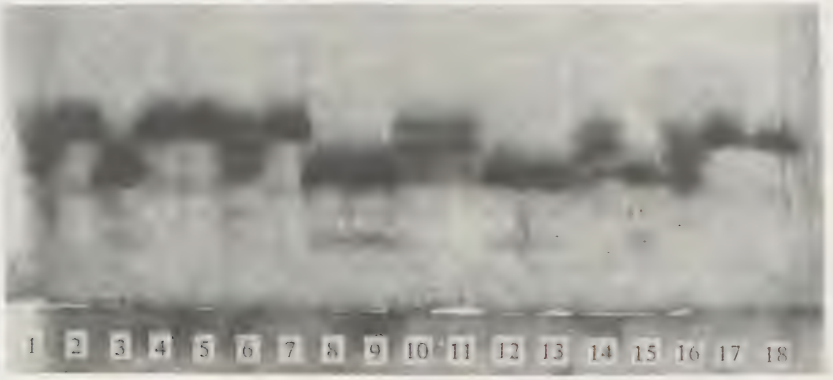

FIG. 2. Glutamate-oxaloacetate transaminase phenotypes in Chongpyung population of *Parafossarulus manchouricus*. Nos. 1-9 = males and 10-18 = females; nos. 2, 4, 5, 7, 17 and 18 = fast/fast band homozygotes; nos. 3, 8, 9, 12, 13 and 15 = slow/slow band homozygotes; nos. 1, 6, 10, 11, 14 and 16 = fast/slow band heterozygotes.

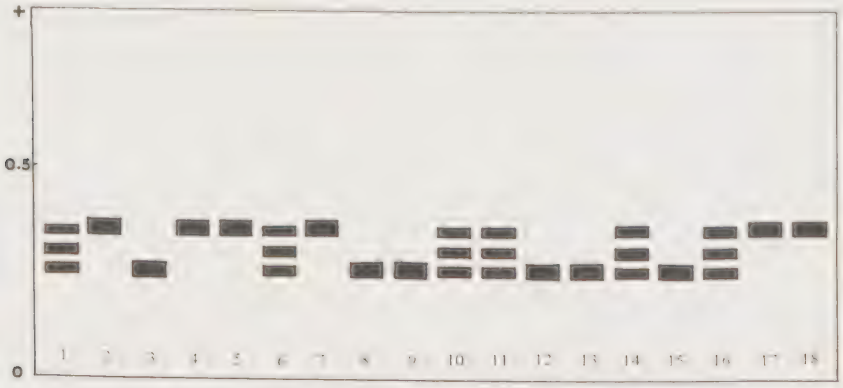

FIG. 3. Drawing of the photograph shown in Fig. 2. + = anodal end of the gel; 0.5 = half-way point between the origin and the front.

interesting to determine if a relationship exists between GOT heterozygosity and susceptibility of *Parafossarulus manchouricus* to *C. sinensis* infection. A correlation between GOT alleles and susceptibility has been suggested by Kitikoon (1982) for the snail *Tricula aperta* and its parasite *Schistosoma mekongi*, where lack of essential free amino acids in the snails' hemolymph (perhaps controlled differentially by different GOT loci) might affect growth of cercariae.

From the above results, it can be noted that the Japanese, Taiwanese and southern Korean populations were monomorphic and homozygous for GOT. One wonders, then, what accounts for the polymorphic and heterozygous nature of the Chongpyung population. Perhaps it is related to the more extreme and variable environment to which the Chongpyung population is exposed.

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SPATIAL AND TEMPORAL CHANGES IN THE DISTRIBUTION OF GASTROPODS IN THE LAM TSUEN RIVER, NEW TERRITORIES, HONG KONG, WITH NOTES ON THE OCCURRENCE OF THE EXOTIC SNAIL *BIOMPHALARIA STRAMINEA*. – The following report centres on the gastropods dwelling on or in the sediments of the Lam Tsuen River, New Territories, Hong Kong. Although a variety of snails, e.g., *Ferrissia* sp. and *Gyraulus chinensis* (Dunker), were associated with emergent plants (e.g., *Eichhornia crassipes* (Martens)), and the prosobranchs *Sinotaia quadrata* (Benson) and *Melanoides tuberculata* (Müller) were found in flooded vegetable plots in the Lam Tsuen Valley, this study includes only those taxa collected from the main channel of the river. Sampling was undertaken at six sites along the river during 1978-79, timed so as to coincide with the main seasonal changes. Additionally, collections were made at seven sites in November 1976, thus allowing an assessment of the ecological effects of increased discharge of agricultural and domestic wastes into the river over the intervening years. It was hoped that this study also would demonstrate how the zonation of gastropods was altered by Hong Kong's seasonal pattern of rainfall, which leads to a marked increase in river discharge volume during the summer months.

The location of the sampling sites along a profile of the river is shown in Fig. 1. Details of the study area will be presented elsewhere (Dudgeon, in prep.). It is sufficient to note here that in 1976 the Lam Tsuen River received small amounts of organic enrichment in the lower course (Stations 5 and 6). However, in 1978-79, a considerable increase in cultural eutrophication was noted with elevated concentrations of dissolved nitrogen and phosphorus compounds, increased Biological Oxygen Demand ($B.O.D._5$), and changes in seston characteristics in the middle and lower parts of the study area. For example, at Station 3 in the middle course, dissolved phosphate concentrations increased between 1976 and 1978-79 by a mean value of 3 times rising to a maximum value of 6 times in March 1979. The values for mean and maximum increases at Station 6 over the same period were 2 and 3 times respectively. Only the characteristics of the uppermost sites (Stations 1 and 2) remained largely unchanged over the study period. Seasonal variations in hydrology and substrate characteristics over 1978-79 were closely related to the rainfall prior to sampling. During the wet season in June and September, concentrations of dissolved nutrients and $B.O.D._5$ test values were reduced. In the dry months, especially in March 1979 when the discharge volume of the river was low, marked increases in these parameters were noted. Increased organic matter in the bottom sediments and the seston was recorded in all but the two upstream sites at this time.

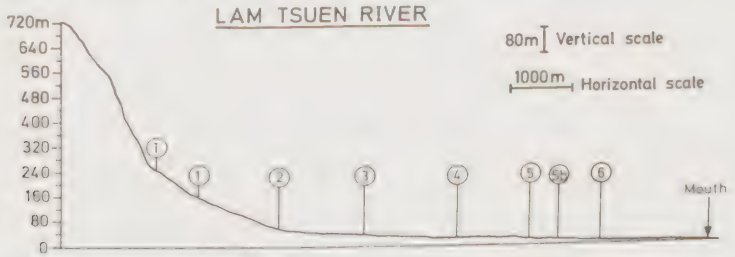

FIG. 1. A profile of the Lam Tsuen River showing the location of sampling Stations 1-6. Site T marks the location of the uppermost permanently flowing section of the river.

Benthos samples were collected by means of stratified (transect) sampling at each site on every visit, unit areas of sediment being collected (down to bed-rock) from close to the bank (two samples) and in the centre of the river (one sample), with two further samples in intermediate positions. These were combined to constitute one collection from a single locality and were considered representative of the benthic microhabitats across the width of a given reach.

In 1976, the abundance and diversity of gastropods in the Lam Tsuen River was low. Only two species were recorded in the study area in 1976. One of these *Brotia hainanensis* (Brot), was restricted to the upper reaches of the river (Stations 1, 2 and 3), a habitat type favoured by this species in running water elsewhere in Hong Kong. *Brotia* sp. has been recorded by Bishop (1973) in the upper tributaries of a Malaysian river, and it is possible that members of this and related genera (Starmühlner, 1979) normally favour habitats where the water is relatively free of suspended solids and flows quickly over stone and boulder substrata. *Radix plicatulus* (Benson) was found in small numbers at Station 4 in 1976. This species is characteristic of lentic habitats in Hong Kong wherever algal food is abundant.

Five snail species were encountered in the Lam Tsuen River during 1978-79: *Brotia hainanensis*, *Radix plicatulus*, *Physella acuta* (Draparnaud), *Hippeutis cantonensis* Yen and *Biomphalaria straminea* (Dunker). Of the two species found in 1976, *B. hainanensis* was restricted to Stations 1 and 2 in 1978-79 (Fig. 2). During the second survey, snails were found at Station 3 only in March 1979, when *P. acuta*, *H. cantonensis* and *R. plicatulus* were very abundant. Both *P. acuta* and *H. cantonensis* occurred at Station 4 between September 1978 and March 1979, but not in June 1978 nor further downstream in September. This was due to 'flushing' of the river during spates caused by the summer rains. The larger numbers of gastropods in the river during 1978-79, particularly in the winter months, was probably linked to an increased food supply as a result of greater organic enrichment of the river. Such a trend was noted by Coetzer (1978) in the Great Berg River, southern Africa. The importance of food supply is suggested by the general tendency of pulmonate populations to extend their upstream ranges as the nutrient concentrations and organic load of the Lam Tsuen River increased during 1978-79. Only Station 6 was occupied by pulmonates in June 1978, but by December Stations 4-6 were extensively colonized (Fig. 2), and in March 1979 pulmonate snails were well established between Stations 3 and 6.

The abundance and diversity of the molluscan assemblage in the Lam Tsuen River increased markedly between 1976 and 1978, with *Brotia hainanensis* showing a restriction in its range whilst *Radix plicatulus* extended the area colonized in 1976. A widespread distribution over 1978-79 was noted for the newly colonizing species *Physella acuta* and *Hippeutis cantonensis*. A third colonizer was the exotic snail *Biomphalaria straminea*, a potential vector

FIG. 2. The distribution and abundance of gastropods in the Lam Tsuen River in 1976 and during 1978-79.

of the blood fluke *Schistosoma mansoni* Sambon in South America. This snail was first found in Hong Kong in 1973 (Meier-Brook, 1974) and subsequently has become widespread in flooded agricultural plots. *B. straminea* was first found in the Lam Tsuen River at Station 6 in June 1978.

All of the species which flourished in the Lam Tsuen River were pulmonates, and it is unlikely that the decrease in water quality during 1978-79 had any deleterious effect upon them. Indeed, Gaufin & Tarzwell (1956) and Harman (1976) have stated that *Physa* [=*Physella*] spp. are associated with culturally eutrophicated waters, and a similar relationship for Lymnaeidae has been noted (Harrison, 1958). Many workers (quoted by Harman, 1976) state that the Planorbidae, Physidae and Lymnaeidae are tolerant of some degree of organic pollution and, on the basis of the present study, some species apparently are favoured by such circumstances. At Station 3, pulmonate numbers were maximal (over 2800 individuals/m^2) when organic enrichment was at its height. Significantly, the addition of sugar to an experimental stream (Warren et al., 1964) encouraged the abundance of snails which may have been feeding upon *Sphaerotilus* (sewage fungus). Increased numbers of *P. acuta*, *Radix plicatulus* and *Hippeutis cantonensis* were noted in the Lam Tsuen River at sites where available food, such as *Sphaerotilus* and filamentous green algae, was abundant.

In conclusion, the organic enrichment of the Lam Tsuen River, and by inference rivers elsewhere in the world, enhances the suitability of the environment for colonization by large numbers of pulmonate snails. As certain pulmonates are important intermediate hosts of schistosomiasis and other parasitic diseases, cultural eutrophication of water courses in regions where such parasites are endemic could become a matter for some concern.

Acknowledgements. Preparation of this manuscript was undertaken with financial support from the United Nations Development Programme/World Bank/World Health Organization Special Programme for Research and Training in Tropical Diseases. Voucher specimens are in the Museum of Zoology, University of Michigan.

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A REPORT ON THE GASTROPOD FAUNA OF AQUARIUM FISH FARMS IN HONG KONG, WITH SPECIAL REFERENCE TO AN INTRODUCED HUMAN SCHISTOSOME HOST SPECIES, *BIOMPHALARIA STRAMINEA* (PULMONATA: PLANORBIDAE). – *Biomphalaria straminea* (Dunker) was first reported as being introduced into Hong Kong by Meier-Brook (1974) and has since arrived in Australia (Walker, 1978) in a consignment of freshwater aquarium fish. The possibility of further spread of this, and other snail species, via exportation of aquarium fish is a very real one, and as part of an ongoing study of the ecology of *B. straminea* in Hong Kong the authors have recorded this species in five aquarium fish farms spread over a wide area of the New Territories of Hong Kong during 1980.

In each case, the snails were found in outdoor concrete ponds, typically in shallow water (less than 15 cm), where fishes such as *Poecilia sphenops* (Cuvier & Valenciennes) (Poeciliidae), *Carrasius auratus* (Linnaeus) (Cyprinidae) and *Corydoras paleatus* (Jenyns) (Callichthyidae) were being reared. A total of eight species of pulmonates were recorded in such situations (Table 1). The hydrology of the ponds (Table 2) was variable, but generally exhibited relatively high levels of calcium hardness compared to other freshwaters in Hong Kong (Dudgeon, 1982). Most sites visited contained a variety of floating plants: *Lemna minor* Linnaeus, *Spirodela polyrhiza* (Linnaeus) (Lemnaceae), *Azolla pinnata* R. Brown (Salviniaceae) and *Eichhornia crassipes* (Martens) (Pontederiaceae), the latter providing the main egg-laying surface for snails in such habitats. The submerged alga *Chaetophora* sp. (Chaetophoraceae) also was present in some localities.

TABLE 1. Incidence of pulmonate gastropods in samples collected from aquarium fish-rearing ponds in Hong Kong[1].

Snail species	% frequency
Biomphalaria straminea (Dunker 1848)	100
Hippeutis umbilicalis (Benson 1836)	20
Gyraulus chinensis (Dunker 1848)	60
Segmentina succinea (Gredler 1884)	60
Ferrissia baconi (Bourguignat 1853)	20
Physella acuta (Draparnaud 1805)	100
Radix plicatulus (Benson 1842)	60
Lymnaea (?Austropeplea) andersoniana (Neville 1877)*	20

[1]Voucher specimens are in the Museum of Zoology, University of Michigan.
*? = *Lymnaea ollula* Gould 1859.

Examination of drainage ditches around the main fish-rearing area (Fanling) indicated that, where such habitats are not polluted by organic wastes (especially pig and chicken feces), *Biomphalaria straminea* and other Planorbidae, as well as Lymnaeidae and Physidae, abounded. In addition, many such ditches supported thriving populations of tropical fish and goldfish, indicating an existing potential for spread of aquatic animals between rearing ponds and other freshwater habitats in the vicinity. All of the pulmonate species found in these ditches were present in the fish-rearing ponds, although the precise composition of the snail fauna of each pond seemed to depend upon the frequency with which draining and cleaning operations were carried out. However, many sites contained several species of snails and as many as seven taxa could be collected from a single pool.

The presence of *Biomphalaria straminea* in aquarium fish farms in Hong Kong, as well as the occurrence of other pulmonates in such situations, will increase the possibility of these species being spread elsewhere on the globe. The United States of America is the largest market for exports of aquarium fish from Hong Kong, and particular care should be taken to avoid introducing a mollusc with the same potential for spread as the Asian clam, *Corbicula fluminea* (Müller) (Sinclair, 1971). Such a danger would seem to be great in countries such as Australia, Singapore and Thailand, which import significant quantities of tropical fish and have climates not dissimilar to that of Hong Kong. Other nations importing aquarium fish from Hong Kong and which have climates potentially suitable for the establishment of *B. straminea* include Argentina, Venezuela, Taiwan, Philippines, Brunei, Malaysia, Sarawak, South Africa, Kenya, Mauritius and Nigeria. If rigorous inspections of shipments of aquarium fish from Hong Kong are not carried out in the recipient countries, the chances of *B. straminea* further increasing its range is, in the opinion of these authors, very great. Also, exporters in the country of origin (e.g., Hong Kong) should

TABLE 2. Hydrological characteristics of aquarium fish-rearing ponds in Hong Kong from which specimens of *Biomphalaria straminea* were collected. All units are in parts per million unless otherwise stated.

Hydrological characteristic	Mean	Maximum	Minimum
Alkalinity	70.00	170.00	0.00
Ammonia	1.14	2.20	0.45
Carbon dioxide	15.60	52.50	3.50
Chloride	100.00	232.00	32.00
Chlorine (free)	0.04	0.10	0.00
Chlorine (combined)	0.02	0.09	0.00
Bromine	0.09	0.22	0.00
Iodine	0.14	0.35	0.00
Chromium (hexavalent)	0.05	0.07	0.04
Copper	0.08	0.16	0.00
Fluorides	0.26	0.46	0.00
Hardness (total)	99.00	156.00	46.00
Hardness (calcium)	76.00	142.00	24.00
Hardness (magnesium)	22.00	42.00	14.00
Iron	0.37	1.22	0.00
Nitrates	4.38	9.72	0.12
Nitrites	0.88	1.25	0.04
Phosphates	0.56	0.90	0.05
Silica	5.58	13.00	0.30
Sulphates	19.58	34.80	6.80
Sulphides	0.01	0.04	0.00
Turbidity (F.T.U.)	39.00	100.00	13.00
pH	7.53	8.50	6.20
Conductivity (μmho)	325.00	485.00	110.00
Oxygen	5.70	8.30	4.70
Temperature (°C)	28.00	30.00	22.00

assume some responsibility for removing snails from consignments of aquarium fish destined for export.

Acknowledgements. This research was undertaken with financial support from the United Nations Development Programme/World Bank/World Health Organization Special Programme for Research and Training in Tropical Diseases. We are grateful to the Trade Development Council (Hong Kong) for data concerning exports of aquarium fish.

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THE ROLE OF NON-CROP PLANTS IN THE PROTECTION OF CROP PLANTS AGAINST THE PESTIFEROUS SNAIL *ACHATINA FULICA*. – **Abstract.** Experimental studies on the efficacy of non-crop plant species, viz., *Cassia sophera, Bryophyllum pinnatum, Synedrella nodiflora* and *Tagetes patula* as detractors in the measures for protection of 10 species of economic plants revealed that the damage by *Achatina fulica* was reduced by 35-77%. Of the four detractor plant species tried, *T. patula* was most effective, while *S. nodiflora, B. pinnatum* and *C. sophera* were next in order of importance.

Introduction. The problem of continued widespread use of pesticides and environmental pollution has forced scientists to look closely into the pest control measures which do not involve the use of poisons. Before the advent of modern synthetic pesticides, man's chief weapon against insects was to disrupt their food plants with a change in crop pattern. Attempts to protect crop plants against insects with inplantation of non-crop plants are again in vogue.

Since physical, chemical and biological pest control programmes failed to meet the challenge of the snail pest *Achatina fulica* Bowdich, we have focused attention on the effect of the introduction of non-crop plants into agricultural practices. Studies on the food-plant preference and feeding behaviour of *A. fulica*, both in the field and under laboratory conditions, revealed that the snails prefer a number of non-crop plants over crop plants as evaluated in the open-air cage environment.

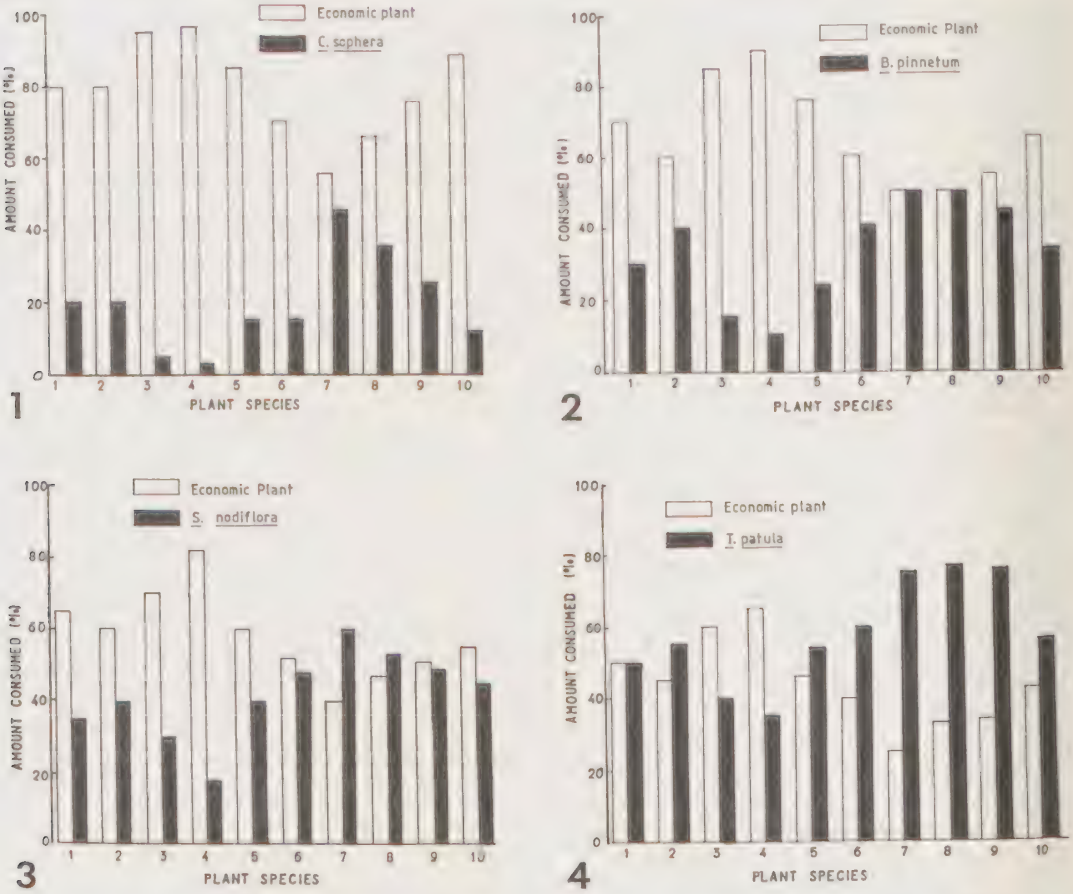
Materials and methods. Four cages measuring 180 x 180 cm and 240 cm high were erected in a shady place on the campus of Calcutta University at Ballygunge. Sized wood, 7.5 x 5.0 cm thick and of appropriate length, was used. The posts were fixed in the soil with concrete bases. The sides and the ceiling were covered with 1-cm mesh expanded metal net. The soil of the floor of the cages was loosened with forks. Voucher specimens are in the Zoological Survey of India, Calcutta (Reg. No. M21622/4).

The monsoon season is at its peak during July-October in West Bengal. The July-August period was selected for our experiments, because the snails are most active then due to intermittent showers, high humidity (90% and above), the temperature range (19-28°C) and poor sunlight. A total of 400 healthy adult *Achatina fulica* between 50-55 mm shell length were collected from their local habitat and 100 individuals were released in each cage on 6 July 1976. To acclimatize the snails, they were supplied with 14 plant species. Ten of these were crop plants, viz., lettuce (*Latuca sativa* Linnaeus), cabbage (*Brassica oleracea* Linnaeus), soybean (*Glycine max* Merr), black bean (*Dolichos lablab* Linnaeus), gourd (*Cucurbita maxima* Duchesne), papaya (*Carica papaya* Linnaeus), tomato (*Lycopersicum esculentum* Mill), cotton (*Gossypium herbaceum* Linnaeus), lady's finger (*Hibiscus esculentus* Linnaeus) and castor (*Ricinus communis* Linnaeus). Four were non-crop plants, viz., *Cassia sophera* Linnaeus (Caesalpiniaceae), *Bryophyllum pinnatum* Aschers and Schweinf (Crassulaceae), *Synedrella nodiflora* Gaertn (Compositae) and marigold, *Tagetes patula* Linnaeus (Compositae). Following acclimatization for a week, one species of non-crop plant was supplied to the snails with only one species of crop plant. Following this procedure, each non-crop species was tried individually against the 10 crop species. Each experiment was repeated for two days. Each day the plants were supplied for a period of 12 hrs, i.e., from 17:00 hrs to 05:00 hrs the next day, the snails' feeding period. The weight of the plant materials initially supplied to the snails was recorded, each weighed separately. The residue was removed on the next morning, weighed, and the amount of each species consumed was determined. The mean amount of consumption was calculated over 100 snails and expressed in percentages. The dead snails were replaced by fresh individuals of the same size. The experiments were completed by 19 August 1976.

Results. In all cases, both the crop and non-crop plants were consumed by *Achatina fulica*, although the rate varied with the combination of the plant species. The snails consumed, 3, 5, 12, 15, 15, 20, 20, 25, 35 and 45% *Cassia sophera* against black bean, soybean, castor, gourd, papaya, lettuce, cabbage, lady's finger, cotton and tomato, respectively (Fig. 1). *Bryophyllum pinnatum* was consumed at the rate of 10, 15, 24, 30, 34, 40, 40, 45, 50 and 50%, respectively, against black bean, soybean, gourd, lettuce, castor, cabbage, papaya, lady's finger, tomato and cotton (Fig. 2). Eighteen, 30, 35, 40, 40, 45, 48, 49, 53 and 60% of *Synedrella nodiflora* was consumed against black bean, soybean, lettuce, cabbage, gourd, castor, papaya, lady's finger, cotton and tomato, respectively (Fig. 3). *Tagetes patula* was consumed at a higher rate, i.e., 35, 40, 50, 54, 55, 57, 60, 75, 76 and 77% against black bean, soybean, lettuce, gourd, cabbage, castor, papaya, tomato, lady's finger and cotton, respectively (Fig. 4). The mortality rate in snails during the period of experiments was similar to that in their natural habitat, where the snails were collected.

Discussion. Investigations on the potentiality of non-crop plants in minimising the damage of crop plants by molluscan pests have not been made so far. It is reported that, though *Achatina fulica* feed exclusively on cultivated plants, they can thrive equally well on wild plants (Mead, 1961; Raut & Ghose, 1982). Survival of the slug *Agriolimax reticulatus* (Müller) on wild vegetation has been reported by Frömming (1954) and Pallant (1969, 1972). The majority of land molluscs in Britain feed harmlessly on wild plants (Chatfield, 1976).

The present study indicates that the damage to economic crop plants caused by *Achatina fulica* can be reduced by 35-77% through the introduction of non-crop plants, viz., *Cassia sophera, Bryophyllum pinnatum, Synedrella nodiflora* and *Tagetes patula*. Of these four non-crop plants, *T. patula* was the most effective, while *C. sophera* was least important. It may be suggested that planting those non-crop



FIGS. 1-4. Influence of four detractor plants in reducing damage to economic plants by *Achatina fulica*. FIG. 1. *Cassia sophora*. FIG. 2. *Bryophyllum pinnatum*. FIG. 3. *Synedrella nodiflora*. FIG. 4. *Tagetes patula*.

1, Lettuce; 2, cabbage; 3, soybean; 4, black bean; 5, gourd; 6, papaya; 7, tomato; 8, cotton; 9, lady's finger; 10, castor.

plants in guard rows, or around the agricultural fields, might be effective in reducing the rate of damage to crop plants by *Achatina fulica*.

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CREPIDULA ONYX INTRODUCED INTO AND ESTABLISHED IN HONG KONG. – The only calyptraeid mollusc recorded from Hong Kong is *Crepidula walshi* Reeve, commensal with hermit crabs (Yipp, 1980). The Calyptraeidae have an almost global distribution, which can be accounted for, in part, by species introduced into regions outside the group's natural range, e.g., *C. fornicata* (Linnaeus) into Europe (Orton, 1912).

Habe & Maze (1970) reported *Crepidula fornicata* introduced into Tokyo Bay, Japan, in 1968. Habe (pers. comm.) now believes this species to be *C. onyx* Sowerby, which subsequently has extensively spread along the southern coast of Japan from Onahama, Honshu, to Shikoku and Kyushu. The natural range of *C. onyx* is the west coast of the Americas from Puntarenas, Costa Rica, to San Pedro, California, and appears little affected by artificial distribution (Hoagland, 1977).

Small numbers of a calyptraeid snail, tentatively identified as *Crepidula onyx*, were collected by the third author in 1979 at Tai Tam Bay (south coast of Hong Kong Island), where they were found attached to intertidal trochid shells. Studies on Hong Kong's fouling communities have hitherto, however, failed to report *C. onyx*, although a benthic survey of Victoria Harbour in 1979 by G.B. Thompson and P.K.S. Shin (pers. comm.) recorded the species at subtidal depths.

We undertook a survey of the fouling community in Victoria Harbour and elsewhere between May and July 1982. Eleven piers (Fig. 1A, 1-11) outside Victoria Harbour were examined; no *Crepidula onyx* were found. At Stations A-H (Fig. 1B, A-H) within Victoria Harbour, however, *C. onyx* was consistently present. Stations A-G comprised cement piers, Station H comprised four local dry-docked vessels. Table 1 shows the dominant members of the fouling community found at each station, the number of fouling species present (as an indication of the maturity of the community) and the number of *C. onyx* recorded/m^2. *C. onyx* is most prevalent at Stations C, D and F where the dominant fouler was *Perna viridis* (Linnaeus). The *C. onyx* ranged in length from 5-53 mm and externally are a dull brown with dark radial lines; the periostracum is rough and fringed. Internally, the shell is a shiny, chocolate brown, although the septum is white, of variable contour and with distinct growth lines. Characteristically, the mantle margin is pigmented with dark radial stripes and has short tentacle-like extensions (Hoagland, 1977), which confirms the identity of the Hong Kong specimens.

Crepidula onyx is a protandric hermaphrodite with a reduction in the relative size of the penis following sex change (Coe, 1942). A large sample of *C. onyx* from Station C was measured along the snails' greatest lengths. Individuals also were sexed (using gamete smears) and inspected for egg masses brooded under the foot. Fig. 2 shows the population to be bimodal, with the larger peak of small individuals (7-12 mm) comprising males or juveniles. The smaller peak of larger individuals (26-36 mm) comprised females; many females were brooding egg capsules. Thus, *C. onyx* from Hong Kong has a pattern of sexuality similar to that reported for this species by Coe (1942). In its natural range, Coe (1942) reported that *C. onyx* forms mating stacks of up to 17 individuals, smaller males apically and larger females basally. This

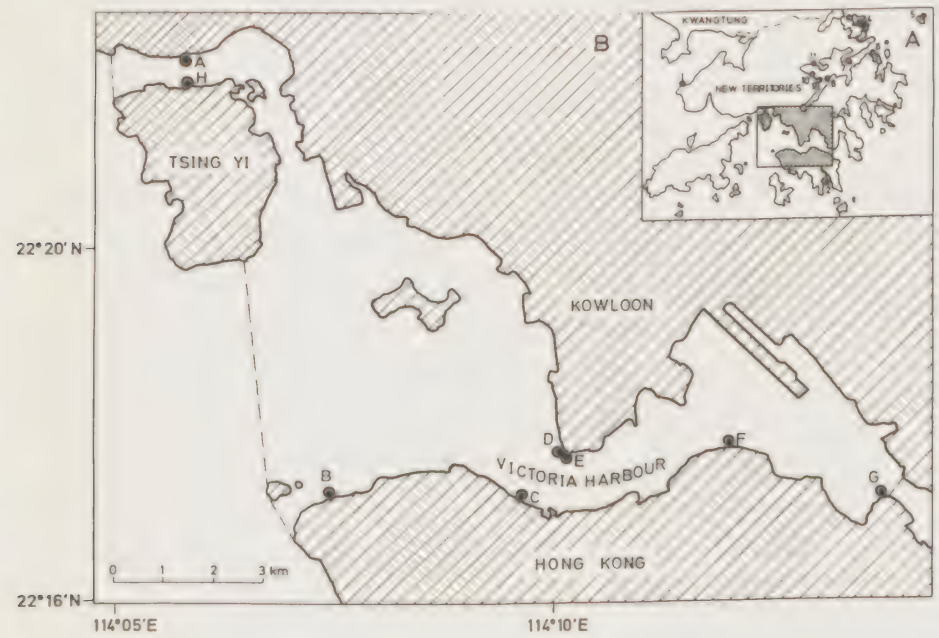

FIG. 1. A, A map of Hong Kong showing Stations 1-11 outside Victoria Harbour where *Crepidula onyx* is absent. B, A map of Victoria Harbour showing the piers A-G and the boatyard (H) where *C. onyx* was present in 1982.

TABLE 1. The number of fouling species present with the dominant fouler at the stations in Victoria Harbour, Hong Kong (see Fig. 1). The numbers of *Crepidula onyx*/m^2 at each station also are given.

Station		No. of fouling species present	Dominant fouler	No. of *C. onyx*/m^2
Piers	A	32	*Alectryonella plicatula*	13
	B	34	*Spongia* sp.; *Schizoporella unicornis*	24
	C	27	*Perna viridis; Crepidula onyx*	994
	D	32	*Perna viridis*	294
	E	25	*Schizoporella unicornis; Spongia* sp.	19
	F	25	*Perna viridis*	488
	G	26	*Balanus reticulatus*	100
Vessels	H_1	27	*Hydroides elegans*	11
	2	23	*Mytilopsis sallei*	12
	3	21	*Balanus amphitrite*	13
	4	22	*Styela plicata*	38

does not occur in Hong Kong. Small, solitary individuals attach to the shells of various gastropods. On *Perna*, however, small groups of sex-mated individuals crowd together, males typically resident on the underlying female.

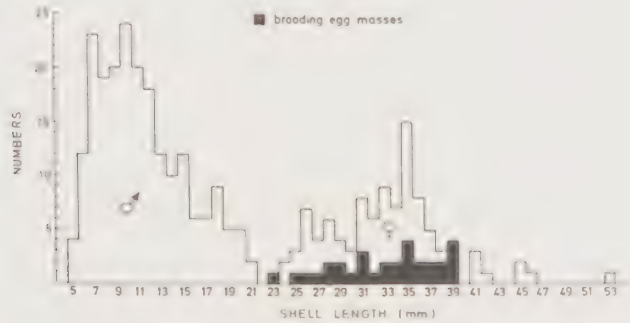

FIG. 2. A histogram of the population structure of *Crepidula onyx* at Station C in Victoria Harbour, Hong Kong.

Possibly *Crepidula onyx* has been introduced into Hong Kong from Japan, sometime prior to 1979. Between 1979 and 1982, it became firmly established in Victoria Harbour, one of the busiest ports in the world, with some 10,000 vessels arriving and departing annually. There is thus a good chance that *C. onyx* may spread even further.

Acknowledgements. We are grateful to Dr. J.D. Taylor (British Museum (Natural History)) and Dr. T. Habe (Tokai University) for confirming the identity of *Crepidula onyx*.

Voucher specimens have been deposited in the Museum of Zoology, The University of Michigan.

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MYTILOPSIS SALLEI (BIVALVIA: DREISSENOIDEA) ESTABLISHED IN VICTORIA HARBOUR, HONG KONG. – *Mytilopsis sallei* (Recluz) is native to Central America (Marelli & Berrend, 1978), where it attaches to stones and algal mats in Mexico and occurs in coastal lagoons in Belize and Venezuela (Robertson, 1963; Escarbassiere & Almeida, 1976). This species was introduced into Visakhapatnam Harbour, India, about 1967 (Ganapati et al., 1971) to the virtual exclusion of the endemic species (Morton, 1981). In April 1980, wreckage of a wooden-hulled boat was washed up on one of Hong Kong's beaches. This was found to be covered by small specimens of *M. sallei*, newly dead (Morton, 1980). The planking was speculated to be the remains of a refugee boat, implying that a population of *M. sallei* existed in waters close to Hong Kong. It also was speculated that, if these individuals (or others arriving at a similar time) had spawned prior to their beaching, *M. sallei* could be established in Hong Kong in the near future. *M. sallei* was introduced into Shimizu Harbour, Japan, in 1974 and Kaoshung Harbour, Taiwan, in 1977 (T. Habe, pers. comm.). Few wooden-hulled boats arrive in Hong Kong from Japan or Taiwan, but, nevertheless, *Mytilopsis* is now reported as established in Hong Kong.

Between 8 May and 28 June 1982, a survey was carried out of fouling organisms in Victoria Harbour, Hong Kong. Sixteen local inshore vessels and seven piers were examined. In three instances, but only from vessels dry-docked at a north Tsing Yi Island boatyard, specimens of *Mytilopsis sallei* were found (Fig. 1), as follows. (1) The hull of a tug "Tsing Chau", previously in the water for 8 months operating close to Hung Hom, Kowloon, had six individuals of *M. sallei*/m^2 with 17 other species of foulers recorded. *Balanus amphitrite amphitrite* was dominant. (2) Marine Department Tug No. 30, abandoned at Tsing Yi, possessed 79 specimens of *M. sallei*/m^2. Of these, 13 were alive; 15 other fouling species were recorded, including *Hydroides elegans, B. reticulatus, Styela plicata* and *S. canopeus*. (3) Lighter No. 10, previously stationed in a typhoon shelter at Tsuen Wan, was heavily infested with 2392 specimens of *M. sallei*/m^2. Of these, 2258 were alive. Twenty-two other fouling species were recorded, but *M. sallei* was dominant, with a wet weight of 2.58 kg/m^2 and 100% cover.

The individuals constituting the samples were measured. An earlier study of *Mytilopsis sallei* in Visakhapatnam (Morton, 1981) established the population structure for this species at that location (Fig. 2A) and showed it to be a rapidly growing, fast maturing opportunist. The sample of *M. sallei* stranded on a Hong Kong beach in 1980 comprised juveniles (Fig. 2B) which, using the growth data for *M. sallei* at Visakhapatnam (Mangapathi Rao et al., 1975), were all less than one month old, re-enforcing the view that they had been brought to Hong Kong from a nearby port.

The Tug No. 30 sample (Fig. 2C) was too small to be meaningful, but the Lighter No. 10 sample (Fig. 2D) comprised a single peak in the size range 1.5-1.8 cm. Using the growth data of Mangapathi Rao et al. (1975), it seems that these animals could have attained this size in two to three months and thus that they probably settled in Spring (April) 1982 and represent the first spawning (in 1982), now considerably grown, of an adult population resident in Victoria Harbour. The samples did not contain older individuals, either because all such vessels require regular cleaning or because Spring 1982 saw the first major spatfall by this newly introduced species. It would appear that, since the infected vessels had never left Victoria Harbour, they had picked up *Mytilopsis sallei* from a recently established resident adult population. There is some significance in the fact that all three vessels were either abandoned at the boatyard at Tsing Yi Island in the western reaches of Victoria Harbour or were based close by. *M. sallei* has not been recorded from elsewhere in the harbour. South of Tsing Yi Island is the Western Quarantine and Immigration Anchorage where all refugee boats are taken. From here they may sold or destroyed; in the latter case, this may be at the typhoon shelter to the east of Tsing Yi Island at Tsuen Wan and, significantly, where Lighter No. 10, the most densely fouled vessel, was based. Should a boat infected with *M. sallei* arrive in Hong Kong, the waters around Tsing Yi would be the anticipated site of initial colonisation (Morton, 1980).

The individuals on the three vessels would be sexually mature (this species maturing early) (Morton, 1981), so it is now certain that a viable population of *Mytilopsis sallei* has been established in Hong Kong, possibly in 1981 following initial introduction in 1980. It seems likely that this introduction (if the focus of the infestation is Tsing Yi) has been by small boats, since ocean-going vessels docking close by are not infected. Import by refugee boats from a port close to Hong Kong is proposed.

With *Mytilopsis sallei* established in Hong Kong (and also Shimizu and Kaoshung), it is clear that the species is going to spread, possibly at an accelerated rate. Approximately 10,000 vessels arrive and depart Hong Kong every year. It is hoped that this spread can be accurately recorded.

Voucher specimens have been deposited in the Museum of Zoology, University of Michigan.

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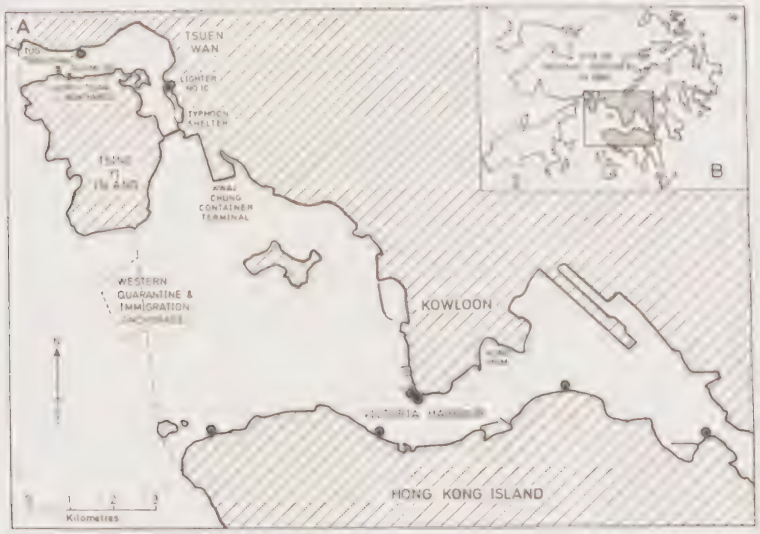

FIG. 1. A map of Victoria Harbour, Hong Kong, showing piers (●) where *Mytilopsis sallei* has not been found and the locations (*) to the north of Tsing Yi Island where three docked vessels were found to be fouled by this bivalve.

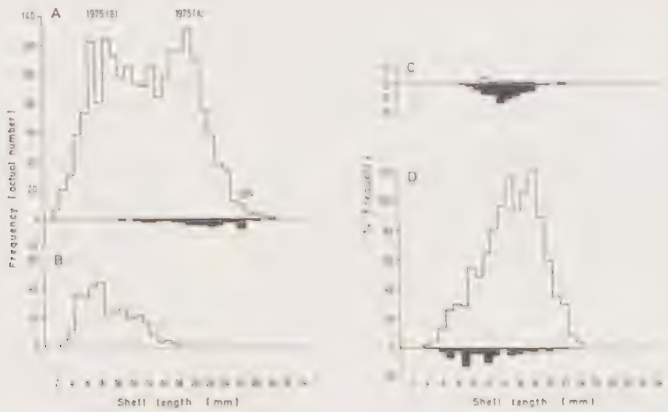

FIG. 2. The population structure of *Mytilopsis sallei*. **A**, A mature population at Visakhapatnam Harbour, India, in July 1975 (after Morton, 1981). **B**, The population on beached boat wreckage at Hong Kong in May 1980 (after Morton, 1980). **C**, The population on Tug No. 30 at Tsing Yi Island in June 1982. **D**, The population on Lighter No. 10 at Tsing Yi Island in June 1982. Upper histograms = living animals; black histograms = empty valves.

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MISCELLANEA

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TWO AMENDMENTS TO CRAMPTON'S MONOGRAPH ON TAHITIAN PARTULIDAE

Yoshio Kondo and J.B. Burch

In 1916, Henry E. Crampton published his monograph: "*Studies on the variation, distribution, and evolution of the genus* Partula *– The species inhabiting Tahiti*." This monograph was a large volume with many colored plates, detailing and analyzing the morphological variation among individuals, and within and among populations, varieties and species of *Partula* on Tahiti (Society Islands). The importance of Crampton's work has been pointed out by Mayr et al. (1953: p. 11) in their *Methods and principles of systematic zoology*.

The present paper summarizes results from an anatomical study of Tahitian Partulidae by the senior author. The study was dictated by the need to establish the reliability of comparative genital anatomy in assessing partulid taxonomy before dealing with partulids collected from other Polynesian islands in 1966-69.

In 1970, the junior author and his assistants collected Tahitian Partulidae (*Partula* and *Samoana*) in 33 of Crampton's 62 valleys. Before dissection, this material was sorted and preliminarily identified by shell criteria according to Crampton's method. Samples were dissected from every valley and all stations of each valley to minimize errors. The total number of animals dissected amounted to 866 and comprised seven species and 12 subspecies.

This work permits the following two amendments to Crampton's distribution maps (Figs. 1 and 2): (1) to *Partula otaheitana sinistrorsa* Pease and *P. o. sinistralis* Pease of southern Tahiti Nui[1] should be added sinistral and dextral *P. affinis producta* Pease (Fig. 1); (2) *P. clara marmorata* Crampton of eastern Tahiti Nui and Tahiti Iti should be cancelled and replaced by *P. hyalina* Broderip (Fig. 2).

In regard to the first modification, i.e., the additional presence of *Partula affinis producta*

TABLE 1. Analysis of 2036 *Partula* from 11 valleys in southern Tahiti Nui in 1970. (All specimens are housed in the Bernice P. Bishop Museum.)

Valley	Subspecies	Sinistral	Dextral	Subspecies	Sinistral	Dextral
Faone*	*P. a. producta*	38	14			
Apirimaue	*P. a. producta*	211	26			
Titaviri	*P. a. producta*	15	220			
Vaihiria	*P. a. producta*	130	–			
Vairaharaha	*P. a. producta*	36	–			
Faarahi	*P. a. producta*	–	29	*P. o. sinistrorsa*	119	–
Vaitunamea	*P. a. producta*	348	–	*P. o. sinistrorsa*	23	–
Taharua	*P. a. producta*	137	–	*P. o. sinistrorsa*	–	7
Papeiti	*P. a. producta*	78	–			
Temarua	*P. a. producta*	155	–	*P. o. sinistralis*	239	14
Terechia	*P. a. producta*	–	13	*P. o. sinistralis*	57	127
Totals		1148 (79%)	302 (21%)		438 (75%)	148 (25%)
		1450 (71%)			586 (29%)	
				2036		

*Oopu Valley between Faone and Aprimaue has *P. affinis affinis* but is not listed here.

[1] Tahiti Nui is the larger northwest part of the island and Tahiti Iti the smaller southeast peninsula.

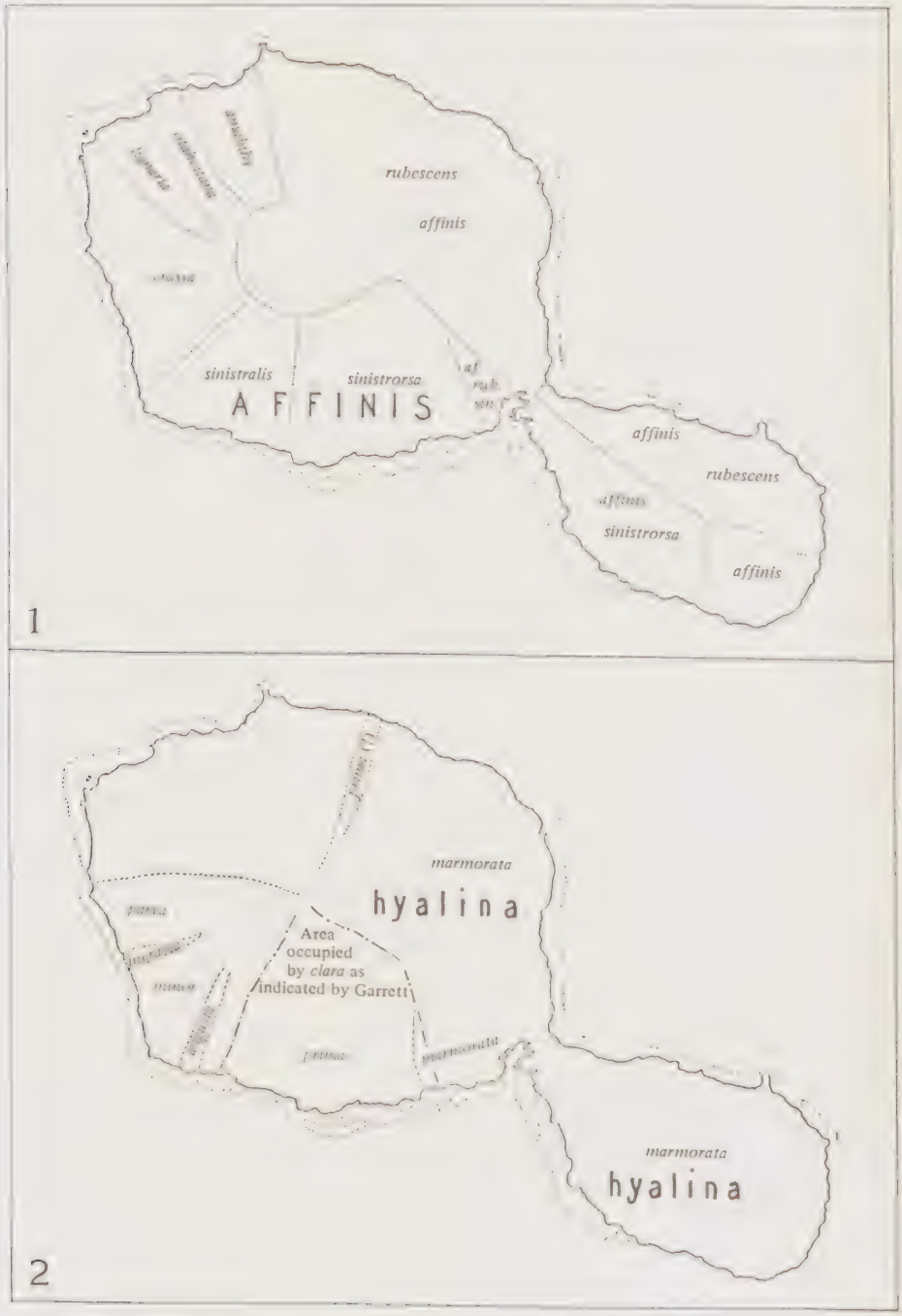
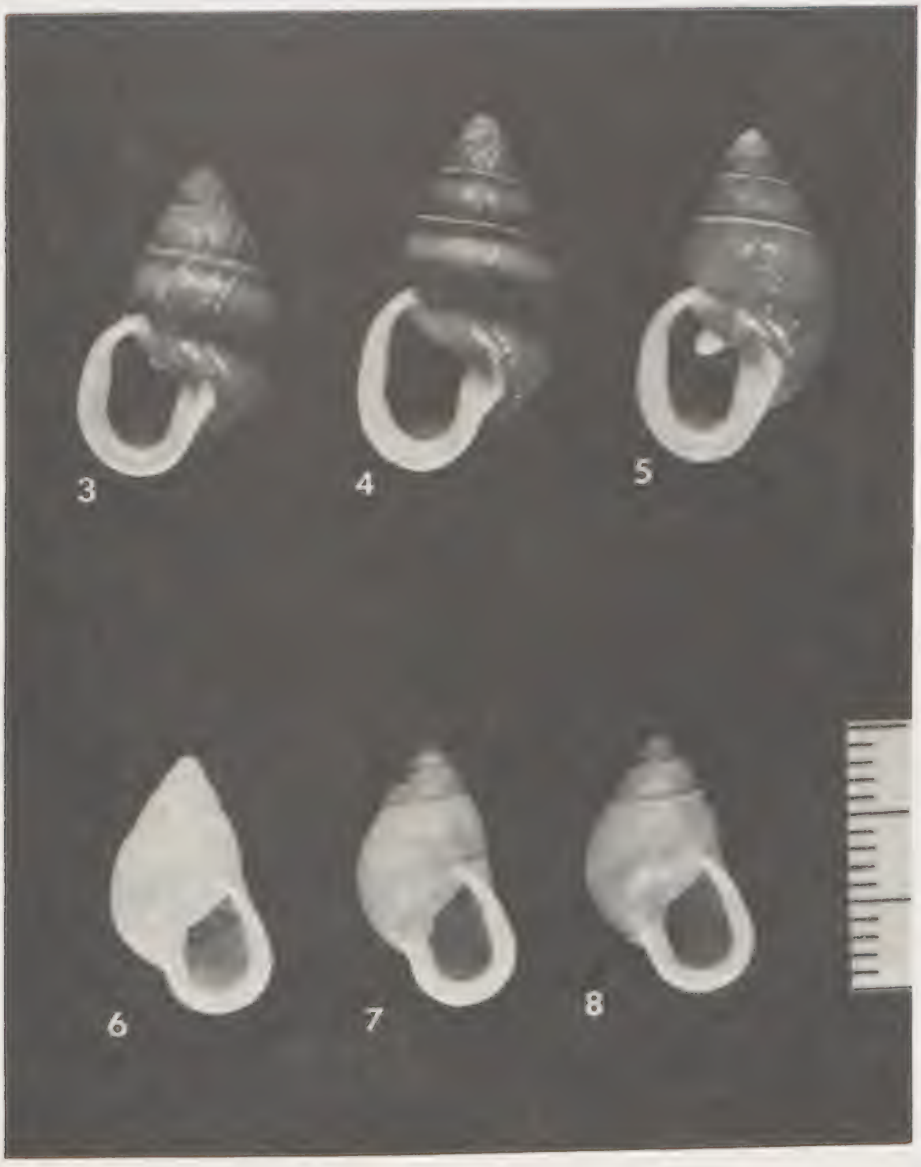


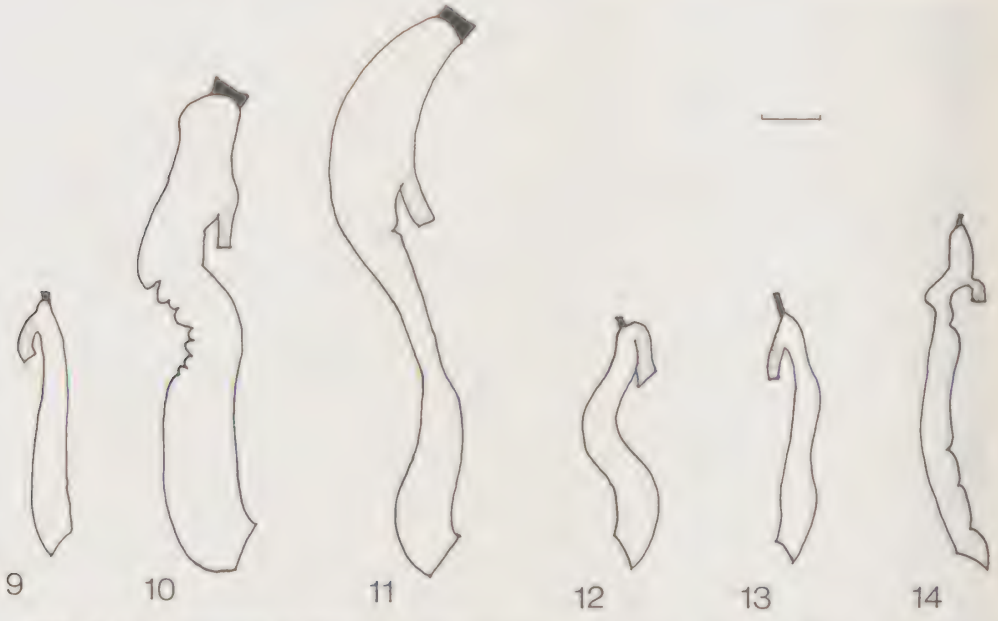
FIG. 1. Distribution of *Partula* on Tahiti: Crampton's (1916: p. 115) text-fig. 7, here amended (capital letters) to include *P. affinis producta* where he recorded *P. otaheitana sinistrorsa* and *P. o. sinistralis* in southern Tahiti Nui. (Map reprinted by permission of the Carnegie Institution of Washington.) FIG. 2. Distribution of *Partula* on Tahiti: Crampton's (1916: p. 62) text-fig. 5, amended (bold letters) to show the taxonomic/nomenclatural change from *P. clara marmorata* to *P. hyalina*. (Map reprinted by permission of the Carnegie Institution of Washington.)



FIGS. 3-8. Shells of pertinent Tahitian Partulidae. FIG. 3. *Partula affinis producta*, Vaitunamea Valley. FIG. 4. *P. otaheitana sinistrorsa*, Vaitunamea Valley. FIG. 5. *P. otaheitana sinistralis*, Temarua Valley. FIG. 6. *P. hyalina*, Haavini Valley. FIG. 7. *P. hyalina* (Crampton's "*clara marmorata*"), Haavini Valley. FIG. 8. *P. clara*, Vaihiria Valley. Scale in mm.

in southern Tahiti Nui, a simple analysis of the 2036 specimens collected by Burch and his team in 1970 in 11 valleys between Faone and Tereehia gives these percentages (see Table 1): *P. a. producta*, 71%; *P. otaheitana sinistrorsa-sinistralis*, 29% [the hyphenated *sinistrorsa-sinistralis* above and elsewhere means that these two "subspecies" cannot be differentiated].

That Crampton recorded the southern sector of Tahiti Nui as being entirely populated with *Partula otaheitana sinistrorsa-sinistralis* is understandable, since he depended entirely upon conchology. By shell characters, it is not possible to differentiate the race of large *P.*



FIGS. 9-14. Silhouettes of phalli of pertinent Tahitian Partulidae. FIG. 9. *Partula affinis producta*, Vaitunamea Valley. FIG. 10. *P. otaheitana sinistrorsa*, Vaitunamea Valley. FIG. 11. *P. o. sinistralis*, Temarua Valley. FIG. 12. *P. hyalina* (reversed), Haavini Valley (note that the vas deferens connects on the phallus apically). FIG. 13. *P. hyalina* (Crampton's "*clara marmorata*"), from the same lot as the specimen illustrated in Fig. 12. FIG. 14. *P. clara*, Vaihiria Valley (note that the vas deferens connects with the phallus subapically, the characteristic that differentiates *P. clara* from closely related *P. hyalina*). Retractor of phallus black; vas deferens stippled. Scale line = 1 mm.

affinis producta (Fig. 3), both dextral and sinistral, from the equally large *P. o. sinistrorsa-sinistralis* (Figs. 4, 5) complex, both dextral and sinistral. (Shape of penis and attachment of vas deferens are shown in Figs. 9-14).

The second amendment and modification (2) is explained very simply in this manner: still depending entirely upon conchology, Crampton apparently decided that all brownish-pink shells closely related to chalk white *Partula hyalina* were *P. clara marmorata*. Genital anatomy separates *P. hyalina* from brownish *P. clara* precisely; and, just as precisely, unites *P. clara marmorata* with *P. hyalina*.

The roots of the present study go back to 1900 when Pilsbry (1900a,b) dissected *Partula rosea* Broderip and "*Achatinella*" [*Partulina*] *dolei* Baldwin and hypothesized that the land snail families Partulidae and Achatinellidae were both very ancient among the Pulmonata.

The need for anatomical investigation is illustrated by the following anecdote. During the senior author's defense of his Ph.D. thesis, Professor Ernst Mayr, of his Doctoral Committee, queried his informal table (Kondo, 1955: p. 154) in which five subspecies of *Partula otaheitana* (as understood by Crampton) were grouped under three types of phalli (see Table 2). Noting that *P. o. sinistrorsa* occurred under two extreme categories, Dr. Mayr queried the reasons for these anomalies. The very unsure reply was that there must be some misnaming, or else that hybridization might have taken place. Dr. Mayr then followed up by asking what Kondo would do to clarify that enigma. Kondo's answer: Go to Tahiti, live very close to the snails, dissect fresh specimens, and conduct hybridization experiments simultaneously. That theoretical plan would have been ideal but was difficult to implement.

The next best solution consisted in a well-organized and systematic collection on Tahiti, which was done by Burch and his team. The taxonomic value of our findings with regard to the male reproductive system was at first mistrusted, but had to be accepted with mounting

TABLE 2. Distribution of three phallic types in five subspecies of *Partula otaheitana* and in *P. affinis* according to Kondo (1955), now annotated.

Type of penis		
faba[1]	*tohiveana*[1]	*hebe*[1]
P. o. otaheitana, Fautaua[2] *P. o. amabilis*, Pohaitara[3] *P. o. rubescens*, Papenoo[4] *P. o. sinistrorsa*, Vavii[5]	*P. o. rubescens*, Pueu[6]	*P. o. sinistrorsa*, Mataiea[7] *P. o. sinistrorsa* ?, Apirimaue[8] *P. o. affinis*, Oopu[9]

[1] *Faba* type = long-clavate; *tohiveana* type = long-vermiform (belongs to column 1 [long-clavate], this series having intermediate phalli); *hebe* type = short-tubular; [2] dextral, BPBM (Bernice Pauahi Bishop Museum) cat. no. 88626; [3] sinistral, BPBM 136962; [4] sinistral, BPBM 145008; [5] sinistral, BPBM 86666; [6] sinistral, BPBM 88915; [7] sinistral, BPBM 81875; [8] sinistral, BPBM 136399; [9] dextral, BPBM 137046.

evidence. The inconsistencies noted earlier were solved by June 1979. The *Partula otaheitana sinistrorsa* of the *hebe* penis type listed in Table 2 can now be placed with certainty in *P. affinis producta*.

Our forthcoming anatomical revision of the Partulidae will not play havoc with Crampton's valuable work. The bulk of Crampton's volume will stand the test of anatomy, with only a few modifications. Apart from the deletion of *Partula clara marmorata* Crampton, already mentioned, two new species of *Samoana* have been added: *S. burchi* Kondo 1973, and, more recently, *S. jackieburchi* Kondo 1981. This latter species has been distinguished from *P. otaheitana rubescens* Reeve (Kondo, 1980) with which it easily can be confused on account of their similar shells (sinistral, with reddish tips). In seven isolated populations, distant from one another, genital anatomy provided clear distinction.

The revised taxonomy of the Tahitian Partulidae is as follows.

Partula hyalina Broderip 1832
Partula clara Pease 1864
Partula affinis affinis Pease 1867
Partula affinis producta Pease 1864
Partula affinis filosa Pfeiffer 1851
Partula affinis nodosa Pfeiffer 1851
Partula affinis cytherea Cooke & Crampton 1930
Partula otaheitana otaheitana Bruguière 1792
Partula otaheitana amabilis Pfeiffer 1846
Partula otaheitana rubescens Reeve 1850
Partula otaheitana sinistrorsa Pease 1863
Partula otaheitana sinistralis Pease 1863
Partula otaheitana crassa Pease 1884
Partula otaheitana lignaria Pease 1864
Samoana attenuata Pease 1864
Samoana burchi Kondo 1973
Samoana jackieburchi Kondo 1981
Samoana diaphana Crampton & Cooke 1953
(accidental introduction from Moorea)

This notice is prompted by two items in Mayr et al. (1953). Commenting on studies of populations that lead to the change from typological species to the polytypic (p. 11), they stated: "Among the malacologists are to be mentioned particularly Kobelt (1881), Gulick (1905), the Sarasins (1899), as well as Crampton whose biometrical studies in the local geographical variations in the genus *Partula* (1916, 1932) have become classical. . . . The result of this work caused the abandonment of the typological species concept. Species were no longer considered as something fixed and uniform, but rather as polytypic, consisting of many subspecies and local populations, each differing from the others and each showing considerable variability within itself."

These same authors (p. 179) also gave good advice to taxonomists and monographers, recommending that when the author of a taxonomic revision had made interesting ecological, evolutionary, or zoogeographic discoveries, he should not conceal these findings in the introduction of a monograph (where it may remain forever buried) but should publish them in a journal where the article would, in turn, draw attention to the monograph.

ACKNOWLEDGEMENTS

Appreciation is noted to the following: Members of the collecting team that assisted the junior author (Burch) with the field work – James N. Cather (The University of Michigan), John B. Burch, Jr. (age 13 in 1970) and Evin Oshima (age 14 in 1970); the Carnegie Institution of Washington for permission to use maps in Crampton's volume, Publication No. 228; the Government of French Polynesia for permission to collect in the Society and Marquesas islands, and to ORSTOM (Office de la Recherche Scientifique et Technique d'Outre Mer) and its Director of 1970, Dr. Henri Lavondes; the National Science Foundation for assistance through grants GB-3974 and GB-6450, 1965-71; and Ernst Mayr, for permission to use his name.

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IDENTIFICATION KEY FOR THE FRESH- AND BRACKISH-WATER SNAILS OF THAILAND*

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Chantima Lohachit and J.B. Burch

INTRODUCTION

The fresh- and brackish-water fauna of Thailand is rich in snails, with some 268 species currently recognized. One hundred and sixty-two of these species have been found in fresh water only, 96 in brackish water only, and 10 species have been found in both fresh and brackish water. These species are grouped into 75 genera, 23 families and six orders. All three subclasses of gastropods, i.e., the Prosobranchia, Opisthobranchia and Pulmonata, are represented. But, as with the fauna in many areas of the world, the taxonomic system for the majority of these mollusks is based almost entirely on characters of their shells, characters which are usually good for taxon recognition, but which may be deceptive in assessing systematic relationships. Also, the relative taxonomic value of shell characters often is especially difficult to interpret at the population, race and species levels. As the Thai snail fauna is studied in greater detail, and with different methods, some changes almost certainly will be necessary in the systematics, particularly in the lower taxonomic categories. This probably will be true especially at the species and varietal levels, but the generic classification probably will need modification as well.

Because of the medical significance of some of the species, an accurate taxonomy of the Thai snail fauna is important. The desired accuracy will come only with further studies. To encourage further research, we have prepared the current identification key. Our objective is to make the elements of the Thai snail fauna easier to recognize. As future changes are made in the taxonomy of the snails, this identification key will have to be revised accordingly.

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*The preparation of this identification key was supported by the United Nations Development Programme/World Bank/World Health Organization Special Programme for Research and Training in Tropical Diseases. The key was prepared as an aid to a course on Southeast Asian medical malacology, and is part of a larger "Guide to the fresh- and brackish-water snails of Thailand".

KEY TO THE HIGHER TAXA AND GENERA OF THE FRESH- AND BRACKISH-WATER SNAILS OF THAILAND[1]

1 Aperture of shell, in life, closed by an operculum[2] (Fig. 12). Subclasses[3] Prosobranchia and Opisthobranchia[4] 2

Aperture of shell not closed by an operculum in life (Fig. 13). Subclass Pulmonata 59

FIG. 12. An operculated snail, i.e., one which carries an operculum attached to its dorsal posterior foot. a, Position of the operculum when the snail is active; b, position of the operculum when the snail has withdrawn into its shell. FIG. 13. A non-operculated snail, i.e., a pulmonate snail (which does not have an operculum at any stage in its life history).

2(1) Shell with a heterostrophic protoconch[5] (Fig. 14a); animal without radula and jaw. Subclass Opisthobranchia, Order Entomotaeniata, Family Pyramidellidae 3

Shell with a normal protoconch (Fig. 14b); animal always with a radula (see Fig. 9). Subclass Prosobranchia 4

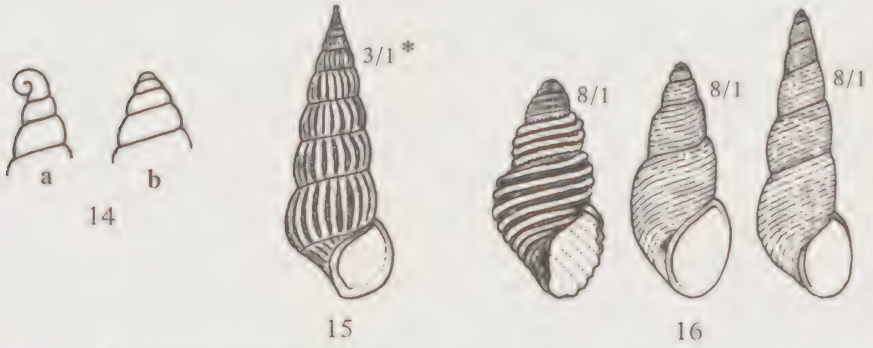

FIG. 14. a, A heterostrophic protoconch at apex of teleoconch; b, a normal (homeostrophic) protoconch. FIG. 15. *Chrysallida*. FIG. 16. *Morrisonietta*.

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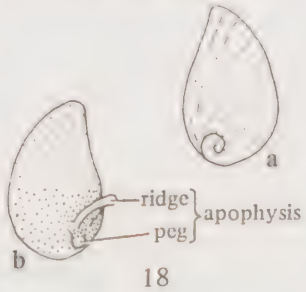
[1] Superscript numbers given in the Key (pp. 108-131) refer to corresponding comments under Notes (pp. 131-132).

*Size of figure to actual size of specimen is given throughout the key by a ratio: 1/1 = natural size; 2/1 = twice natural size; 3/1 = enlarged three times; etc.

3(2) Shell with prominent axial ribs; whorls not shouldered (Fig. 15). Brackish water . . . . . Genus *Chrysallida*

Shell without axial ribs; sculptured with spiral lines or lirae; whorls generally shouldered (Fig. 16). Brackish water . . . . . Genus *Morrisonietta*

17



18

FIG. 17. Neritiform shell in side (spire), top and bottom (apertural) views. FIG. 18. Operculum of a neritid shell. a, External view; b, inner surface (which in life is attached to the dorsal foot).

4(2) Shell either neritiform (i.e., with relatively very large body whorl and very small coiled spire; Fig. 17) or limpet-like with a coiled apex (Fig. 19); operculum with an elongate attachment process (apophysis) on its inner surface (Fig. 18). Order Neritacea[6], Superfamily Neritoidea[7], Family Neritidae[6] 5

Shell not neritiform, spire generally pronounced; or if limpet-like, without coiled apex; inner surface of operculum relatively smooth, or with low ridges[8], but without an elongate attachment process (apophysis) on its inner surface. Orders Mesogastropoda and Neogastropoda 10

5(4) Shell limpet-like, almost bilaterally symmetrical. Brackish water . . . . . Genus *Dostia*

Shell not limpet-like, with typical gastropod spiral symmetry 6

19

20

FIG. 19. *Dostia*. FIG. 20. *Neritilia*.

6(5) Apophysis of operculum long and curved, not divided into peg and ridge. Fresh water . . . . . Genus *Neritilia*

Apophysis of operculum divided into a peg and ridge (Fig. 18) 7

7(6) Adult shell small to medium, less than 15 mm in length (Fig. 21). Brackish water . . . . . Genus *Clithon*

Adult shell medium in size, more than 15 mm in length 8

FIG. 21. *Clithon.* FIG. 22. *Nerita.*

8(7) Palatal wall of shell aperture serrate (Fig. 22). Brackish water . . . . . Genus *Nerita*

Palatal wall of shell aperture smooth 9

9(8) Left anterior edge of septum reflected toward the columella (sometimes the point of this reflection appears as a "tubercle"); ridge of apophysis with grooves and with serrate outer margin (Fig. 23). Brackish water . . . . . Genus *Neritodryas*

Left anterior edge of septum not reflected toward the columella; ridge of apophysis not grooved and serrated (Fig. 24). Fresh and brackish water . . . . . Genus *Neritina*

FIG. 23. *Neritodryas.* a, Shell; b, operculum. FIG. 24. *Neritina.*

10(4) Anterior end of shell developed into a siphonal canal or notch (Fig. 25). Order Mesogastropoda, in part (Superfamily Vermetoidea, in part: Potamididae and Triphoridae), and Order Neogastropoda 11

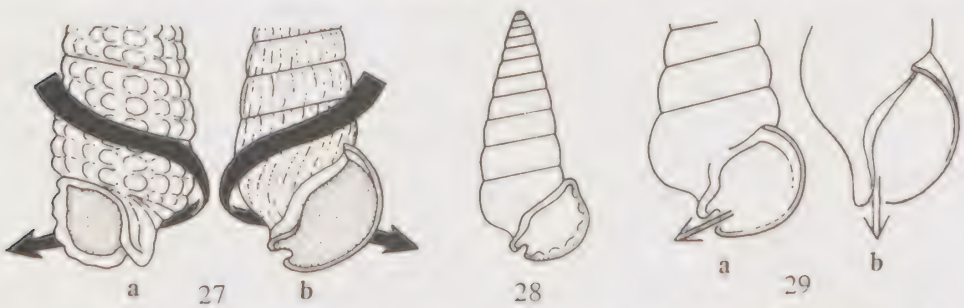
Anterior end of shell not developed into a siphonal canal or notch (Fig. 26). Order Mesogastropoda, in part[9] 18

25 26

FIG. 25. Siphonal canal and notches in the anterior end of some mesogastropod shells.
FIG. 26. Anterior ends of mesogastropod shells without siphonal canals or notches.

11(10) Shell sinistral, i.e., coiled to the left (Fig. 27a). Family Triphoridae. Brackish water . . . . . Genus *Triphora*

Shell dextral, i.e., coiled to the right (Fig. 27b) 12



a 27 b 28 29

FIG. 27. a, A sinistral (left-coiled) shell; b, a dextral (right-coiled) shell. FIG. 28. Cerithiaform shell. FIG. 29. a, Siphonal indentation in shell directed to the left; b, siphonal indentation directed anteriorly.

12(11) Shell cerithiaform (Fig. 28), i.e., turrited, with the aperture flared on either the left or right sides, or both, and the siphonal canal or notch directed to the left (Fig. 29a), not anteriorly (except in *Faunus*; see Fig. 32). Family Potamididae. Mainly brackish water (only one species, *Faunus ater*, also occurs in fresh water) 13

Shell not cerithiaform, spire turrited or depressed, but without flared aperture; siphonal canal directed anteriorly (Fig. 29b). Order Neogastropoda 16

13(12) Shell with prominent transverse (axial) sculpture; aperture with reflected palatal lip 14

Shell with growth lines but without transverse (axial) sculpture; aperture without reflected lip 15

14(13) Shell larger, adults more than 60 mm in length; spiral sculpture consists of narrow grooves (Fig. 30). Fresh and brackish water . . . . . Genus *Terebralia*

Shell smaller, adults less than 60 mm in length; spiral sculpture predominantly of cords and nodules (Fig. 31). Brackish water . . . . . Genus *Cerithidea*

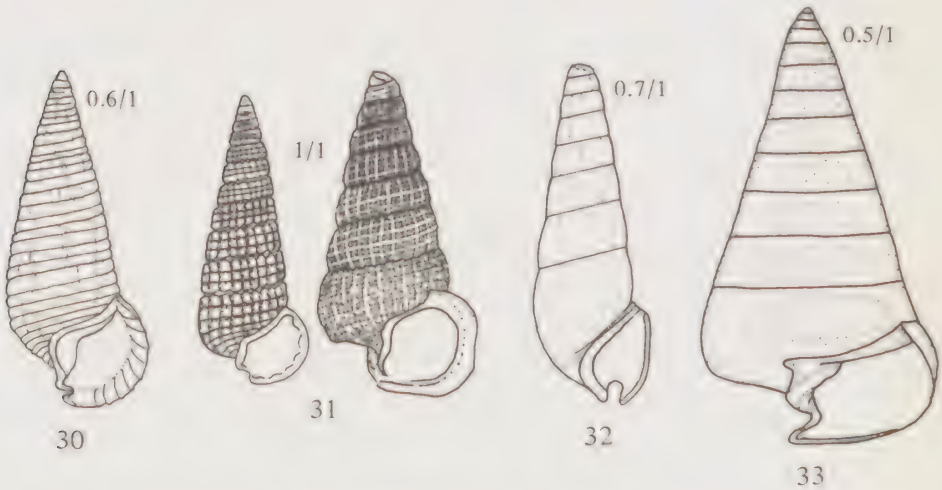


FIG. 30. *Terebralia*. FIG. 31. *Cerithidea*. FIG. 32. *Faunus*. FIG. 33. *Telescopium*.

15(13) Shell narrowly conic, with very weak spiral sculpture; siphonal notch directed anteriorly; aperture also with a posterior notch; columella without folds (Fig. 32). Fresh and brackish water . . . . . Genus *Faunus*

Shell elongately conic, with strong spiral sculpture; siphonal notch directed to the left; aperture without a posterior notch; columella with two folds (Fig. 33). Brackish water . . . . . Genus *Telescopium*

16(12) Shell smooth, ear-shaped in apertural view, spire only slightly raised above the body whorl; operculum lacking. Superfamily Volutoidea, Family Marginellidae (Fig. 34). Fresh water . . . . . Genus *Rivomarginella*

Shell with sculptured surface, not ear-shaped, with high spire; operculum present 17

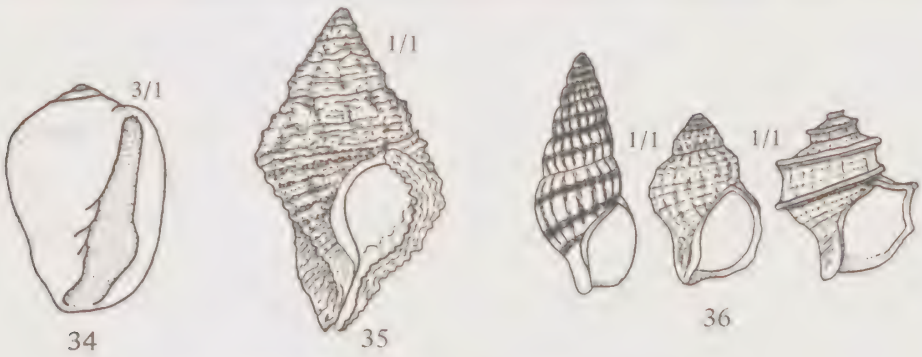


FIG. 34. *Rivomarginella*. FIG. 35. *Chicoreus*. FIG. 36. *Clea*.

17(16) Shell spindle-shaped, with periodic varices; siphonal canal long and narrow. Superfamily Muricoidea, Family Muricidae (Fig. 35). Brackish water . . . . . Genus *Chicoreus*

Shell turrited and conical or subovate, without varices; siphonal canal short and broad (Fig. 36). Superfamily Buccinoidea, Family Buccineidae. Fresh water . . . . . Genus *Clea*

18(10) Shell large, adults more than 40 mm and up to 100+ mm in length, globose, subglobose or oval; spire usually depressed, less than ½ the total shell length; aperture elongate, not round. Superfamily Ampullarioidea, in part: Family Ampullariidae (Fig. 37). Fresh water . . . . . Genus *Pila*

Shell large to small, but if large (i.e., more than 40 mm in length), the spire is elongate, more than ½ the total shell length and the aperture is round or nearly so, not elongate 19

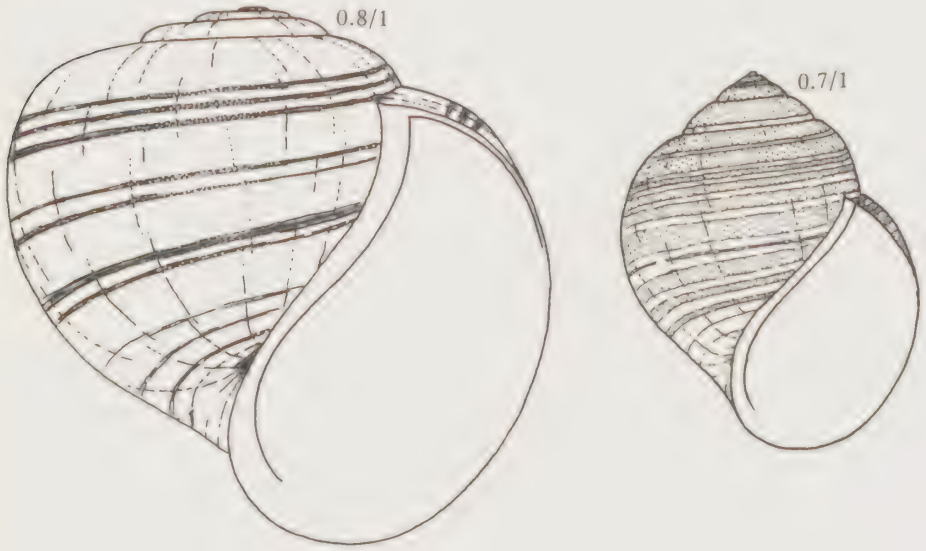


FIG. 37. *Pila*.

19(18) Shell medium, adults 15 to 30 mm in length, ovately or subovately conic with acutely pointed apex and very flattened whorls, sculptured with spiral grooves and generally marked with color patterns. Superfamily Littorinoidea, Family Littorinidae (Fig. 38). Brackish water . . . . . Genus *Littorinopsis*

Shell large to minute, of various shapes, but if ovately or subovately conic with acutely pointed apex and very flattened whorls, then the adult shells are small and less than 10 mm in length 20

38

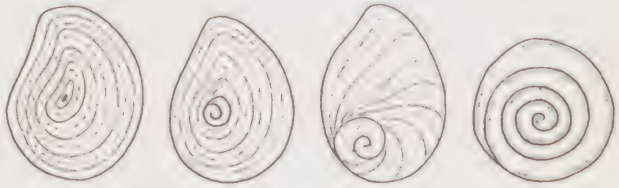


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FIG. 38. *Littorinopsis*. FIG. 39. Types of opercula. a, Concentric; b, concentric with spiral nucleus; c, paucispiral; d, multispiral.

20(19) Operculum concentric (Fig. 39a, b), with or without a spiral nucleus 21

Operculum paucispiral (Fig. 39c) or multispiral (Fig. 39d) 34

21(20) Operculum corneous, entirely concentric (Fig. 39a) 22

Operculum corneous or calcareous, with a spiral nucleus (Fig. 39b) 31

22(21) Shell medium to large, narrowly subovately to widely conic, smooth or with spiral sculpture, but without transverse sculpture; operculum without prominent ridges on the inner side. Superfamily Ampullarioidea, in part: Family Viviparidae[10] 23

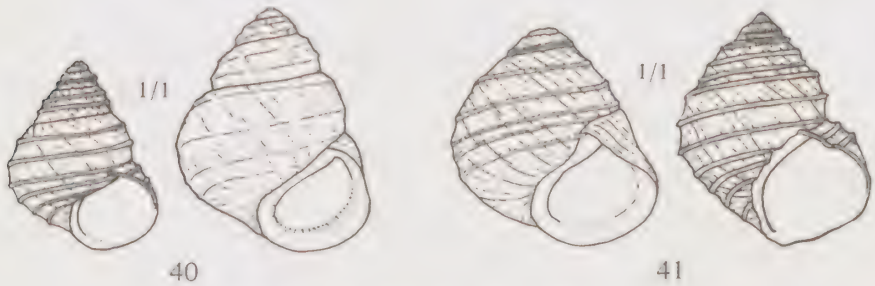
Shell small, narrowly or elongately conic, with strong spiral or transverse sculpture; operculum with one or several prominent inner ridges (Fig. 48a). Superfamily Truncatelloidea, in part: Family Iravadiidae 30

23 (22) Shell lirate, generally with well-developed spiral ridges; lirae occur not only on the posterior ("upper") half of each whorl, but on the anterior ("basal") half as well 24

Shell smooth, or with only very weak spiral ridges, or with one peripheral carina; lirae absent from anterior ("basal") half of whorls 25

24(23) Shell subovately or ovately conic (Fig. 40). Fresh water . . . . . Genus *Sinotaia*

Shell subglobosely or globosely conic (Fig. 41). Fresh water . . . Genus *Anulotaia*



40 41

FIG. 40. *Sinotaia.* FIG. 41. *Anulotaia.*

25(23) Shell narrowly ovately to ovately conic, or if subglobosely or globosely conic, then without peripheral angle or keel 26

Shell subglobosely, globosely or depressed conic, with angular or keeled periphery 29

26(25) Shell generally with spiral color bands (at least some individuals of every population are banded), or, if from unbanded populations, shells are dark olive and longer than 30 mm (Fig. 42). Fresh water . . . . . Genus *Filopaludina*

Shell seldom with spiral color bands, other than a single, purple suprasutural spire band in some species 27

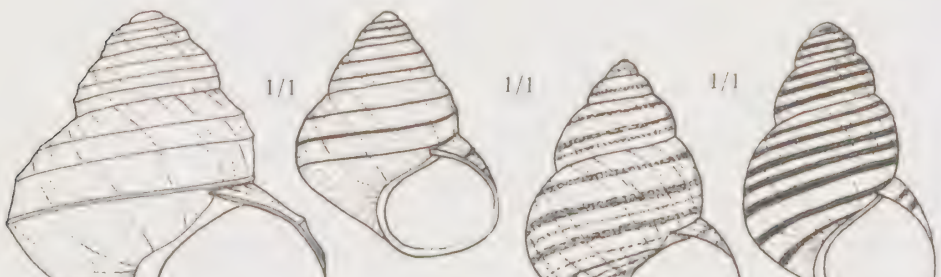


FIG. 42. *Filopaludina.*

27(26) Shell generally thick, solid; embryonic shell without peripheral angle or obtuse carina[11]; outer marginal teeth without cusps (Fig. 43). Fresh water . . . . . Genus *Mekongia*

Shell relatively thin; embryonic shell with a peripheral angle or obtuse carina; outer marginal teeth with cusps 28

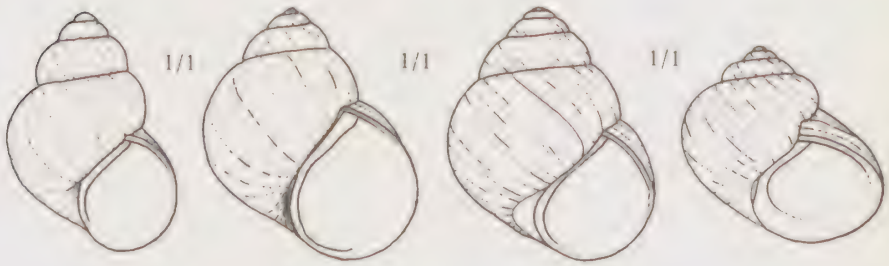


FIG. 43. *Mekongia.*

28(27) Umbilicus open or perforate, funiculate, usually bordered by an angle or distinct carina (Fig. 44). Fresh water . . . . . Genus *Idiopoma*

Umbilicus perforate, not bordered by an angle or carina (Fig. 45). Fresh water . . . . . Genus *Cipangopaludina*

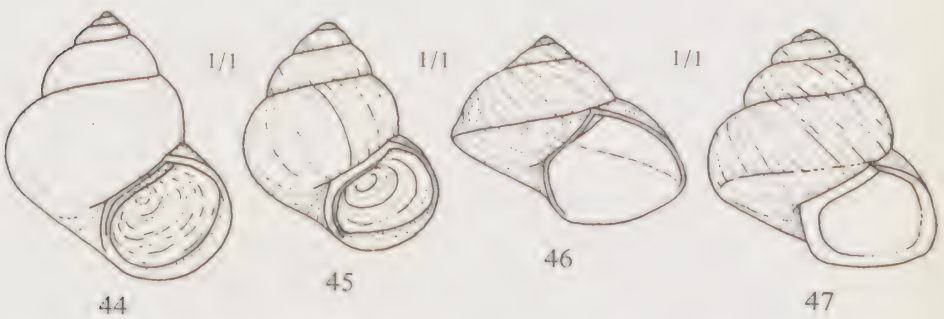


FIG. 44. *Idiopoma.* FIG. 45. *Cipangopaludina.* FIG. 46. *Eyriesia.* FIG. 47. *Trochotaia.*

29(25) Shell rather thin; aperture large, its length about ½ the shell length; one or two spiral ridges between peripheral keel and suture (Fig. 46). Fresh water . . . . . Genus *Eyriesia*

Shell thicker, solid; aperture length less than ½ the shell length; shell without spiral ridges (other than the peripheral keel) (Fig. 47). Fresh water . . . . . Genus *Trochotaia*

30(22) Shell with both spiral and transverse sculpture, surface generally covered with nodules (Fig. 48). Brackish water . . . . . Genus *Iravadia*

Shell with spiral sculpture, but without transverse sculpture; periostracal spines also may be present (Fig. 49). Brackish water . . . . . Genus *Fairbankia*

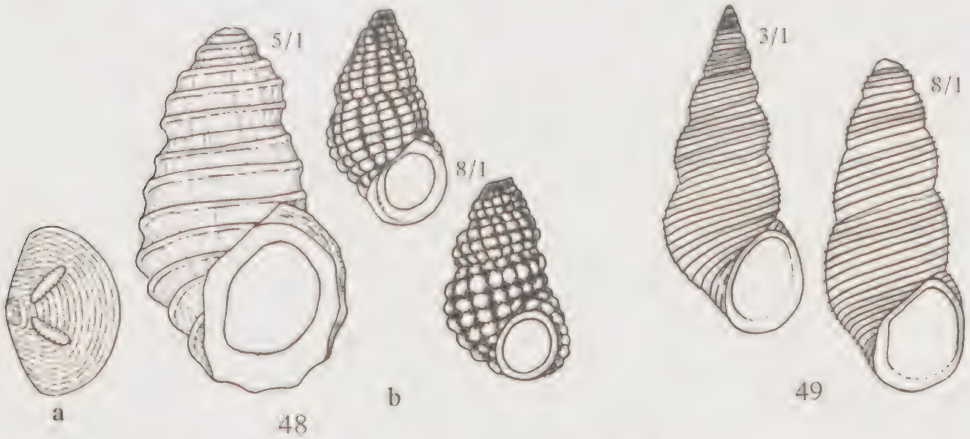


FIG. 48. *Iravadia.* a, Operculum; b, shells. FIG. 49. *Fairbankia.*

31(21) Shell elongate, without spiral color bands; operculum calcareous. Superfamily Ampullarioidea, in part: Family Bithyniidae 32

Shell elongate or subglobose, generally with spiral color bands; operculum corneous. Superfamily Vermetoidea, in part: Family Paludomidae (Fig. 50). Fresh water . . . . . Genus *Paludomus*

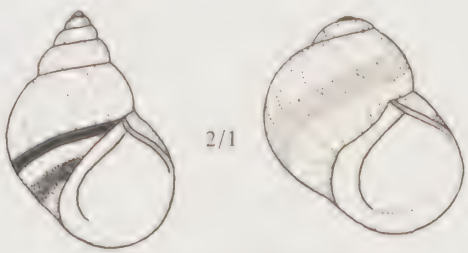


FIG. 50. *Paludomus.*

32(31) Last whorl terminated with a varix (Fig. 51). Fresh water . . . Genus *Hydrobioides*

Last whorl terminated without a varix 33

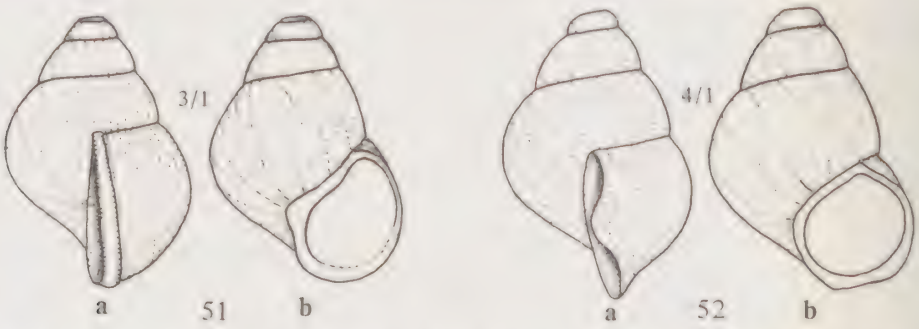


FIG. 51. *Hydrobioides.* a, Side view of shell showing varix; b, apertural view of shell.
FIG. 52. *Wattebledia.* a, Side view of shell showing flange; b, apertural view of shell.

33(32) Outer part of last whorl extended as a flange (Fig. 52a), giving the outer (palatal) lip a sinuous shape (Fig. 52). Fresh water . . . . . Genus *Wattebledia*

Outer part of last whorl not extended as a flange (Fig. 53). Fresh water . . . . . Genus *Bithynia*

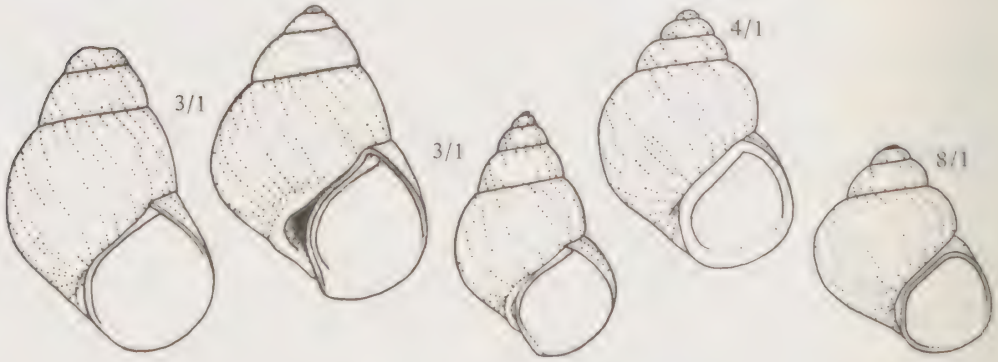


FIG. 53. *Bithynia.*

34(20) Adult shells small to minute, with only several species ranging into the medium size class. Superfamily Truncatelloidea, in part 35

Adult shells medium to very large. Superfamily Vermetoidea, in part: Family Thiaridae 51

35(34) Shell depressed conic, minute, thin, glossy and transparent. Family Tornidae. Brackish water . . . . . Genus *Chamlongia*

Shell not depressed conic, or if so, then it is larger, thick and opaque 36

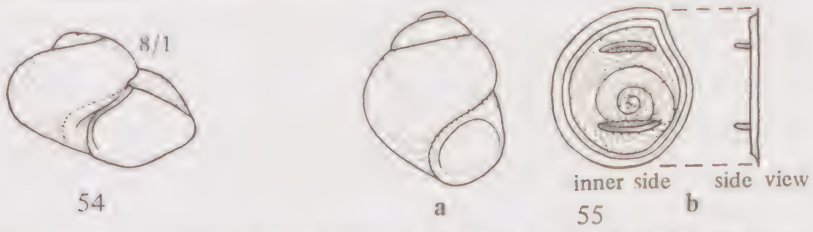


FIG. 54. *Chamlongia*. FIG. 55. Stenothyridae. a, Stenothyraform shell; b, operculum.

36(35) Shell stenothyraform, i.e., the last part of the body whorl and aperture are deflected and reduced in size (Fig. 55a); operculum with three ridges on its inner surface (Fig. 55b). Family Stenothyridae 37

Shell not stenothyraform, i.e., its entire body whorl and aperture follow the snails' initial spiral symmetry and gradual increase in size; operculum without ridges on its inner surface 38

37(36) Shell strongly stenothyraform (Fig. 56). Fresh and brackish water . . . . . Genus *Stenothyra*

Shell weakly stenothyraform (Fig. 57). Fresh and brackish water . . . . . Genus *Gangetia*

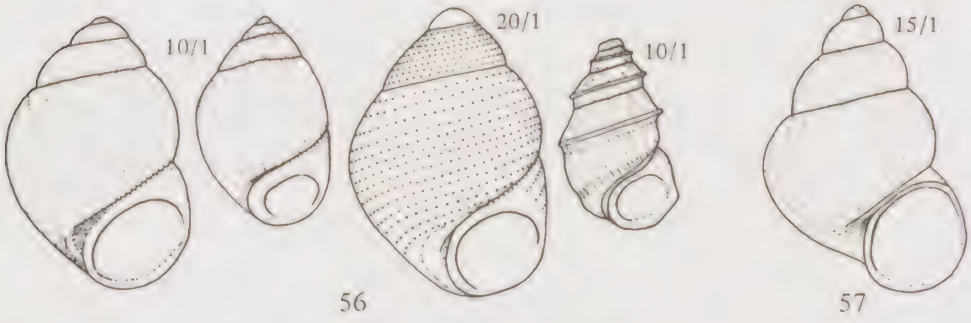


FIG. 56. *Stenothyra*. FIG. 57. *Gangetia*.

38(36) Tentacles rudimentary, reduced to merely short eye-stalks; shell often with color bands, simple, generally ovately or subovately conic, but it also may be elongately or subglobosely conic or subglobose. Family Assimineidae[12] 39

Tentacles well developed; shell variously shaped and sculptured, but without color bands 41

39(38) Shell generally with spiral threads and/or spiral grooves or with reticulate sculpture (Fig. 58). Brackish water . . . . . Genus *Assiminea*

Shell generally smooth or rarely with axial sculpture 40

FIG. 58. *Assiminea.*

40(39) Shell unicolored, brownish-corneous; periomphalum without carina (Fig. 59). Brackish water . . . . . Genus *Paludinella*

Shell with brownish bands, opaque; periomphalum with carina (Fig. 60). Fresh and brackish water . . . . . Genus *Cyclotropis*

FIG. 59. *Paludinella.* FIG. 60. *Cyclotropis.*

41(38) Shell with closely set spiral lines or grooves and without transverse sculpture (other than growth lines); central radular tooth with basal cusps arising only from the lateral angle (Fig. 61a). Family Hydrobiidae 42

Shell variously sculptured, but without closely set spiral lines or grooves; central radular tooth with basal cusps arising from the face of the tooth as well as the lateral angle (Fig. 61b). Family Pomatiopsidae 43

FIG. 61. Central radular tooth of truncatelloid snails. a, A hydrobiid, with basal cusps on a thickened ridge along the lateral angle of the tooth; b, a pomatiopsid, with basal cusps on the antero-posterior ridges.

42(41) Shell planorboid (Fig. 62). Fresh and brackish water . . . . . Genus *Clenchiella*

Shell ovately or elongately conic (Fig. 63). Fresh and brackish water . . . . . Genus *Rehderiella*

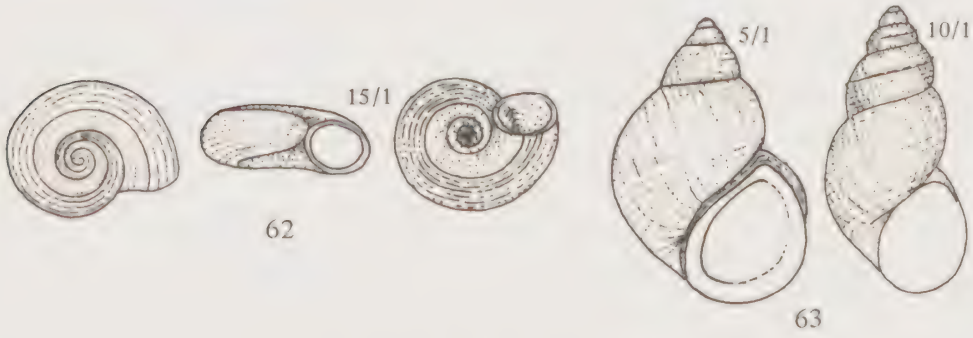


FIG. 62. *Clenchiella.* FIG. 63. *Rehderiella.*

43(41) Shell globose or subglobose, or subglobosely to widely conical, or with very depressed spire 44

Shell narrowly conical to ovately conical, with elongated spire 45

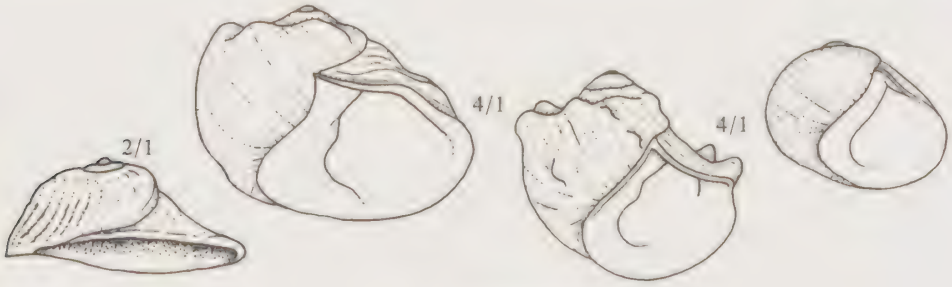
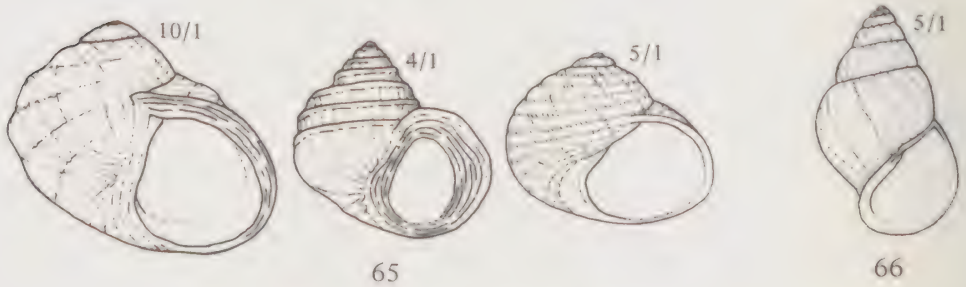


FIG. 64. *Lacunopsis.*

44(43) Apertural columella flattened, sometimes broadly so, with a tendency to form a shelf in the aperture (Fig. 64). Fresh water . . . . . Genus *Lacunopsis*

Apertural columella not especially flattened, and without a tendency to form a shelf in the aperture (Fig. 65). Fresh water . . . . . Genus *Jullienia*



65 66

FIG. 65. *Jullienia.* FIG. 66. *Halewisia.*

45(43) Shell smooth, sculptured with normal growth lines; columellar lip of the aperture noticeably flared (Fig. 66). Fresh water . . . . . Genus *Halewisia*

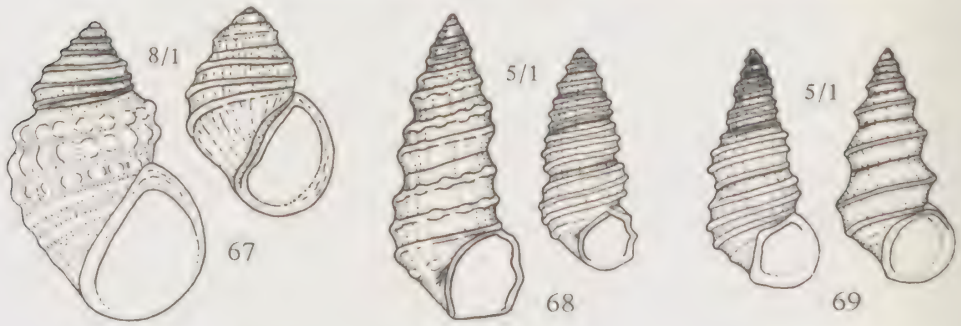
Shell smooth or sculptured with ridges, tubercles, etc.; columellar lip of the aperture not noticeably flared 46

46(45) Shell characteristically with strong spiral sculpture, or if smooth or nearly so, then elongately or narrowly conic and with a flared aperture 47

Shell with transverse (axial) sculpture, occasionally with a weak spiral sculpture, or smooth, but if smooth and narrowly or elongately conic, then without a flared aperture 48

47(46) Shell narrowly subovately to ovately conical (Fig. 67). Fresh water . . . . . Genus *Hydrorissoia*

Shell narrowly or elongately conical, turrited. Fresh water . . . . . Genera *Karelainia* (Fig. 68) and *Paraprososthenia* (Fig. 69)[13]



67 68 69

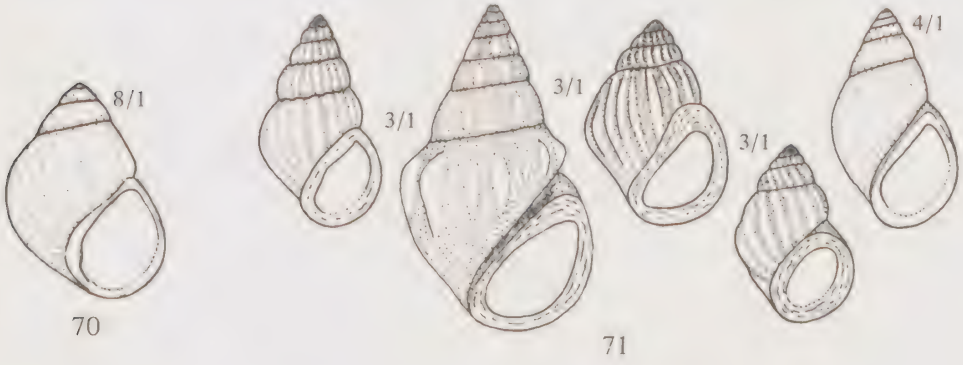
FIG. 67. *Hydrorissoia.* FIG. 68. *Karelainia.* FIG. 69. *Paraprososthenia.*

48(46) Lip of shell aperture noticeably thickened 49

Lip of shell not noticeably thickened 50

49(48) Shell smooth, adult shell length less than 4 mm (Fig. 70). Fresh water . . . . . Genus *Pachydrobiella*

Shell generally with transverse (axial) sculpture, adult shell length nearly always more than 4 mm (Fig. 71). Fresh water . . . . . Genus *Pachydrobia*

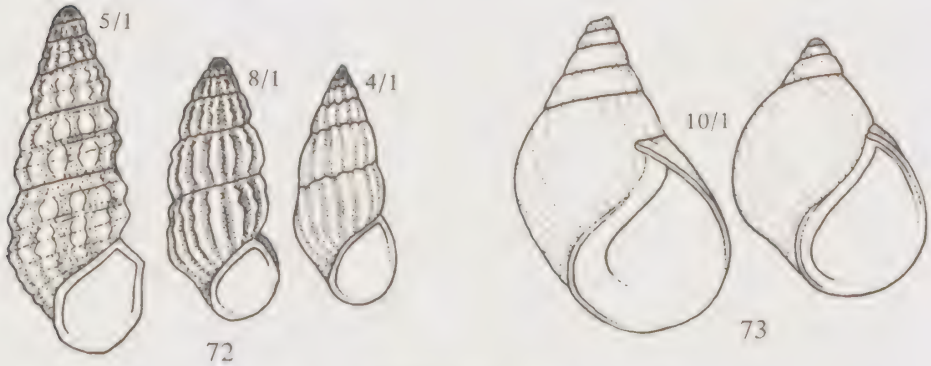


70 71

FIG. 70. *Pachydrobiella.* FIG. 71. *Pachydrobia.*

50(48) Shell generally turrited; most species have well-developed axial sculpture; spire convexly curved (Fig. 72). Fresh water . . . . . Genus *Hubendickia*

Shell elongately or ovately conic, smooth; spire periphery nearly straight or concavely curved (Fig. 73). Fresh water . . . . . Genus *Tricula*



72 73

FIG. 72. *Hubendickia.* FIG. 73. *Tricula.*

51(34) Adult shell large, more than 4 cm and up to 7 cm or more in length, elongately conic; surface sculptured with ribs, spiral cords or carinae, or low spines, or with two or more of these features in common; operculum multispiral (Fig. 74). Fresh water . . . . . Genus *Brotia*

Adult shell medium (1.5-3 cm in length) to large (3.5-7+ cm in length), but if large the shell is without spines, narrowly conic; shells smooth or variously sculptured; operculum multispiral or paucispiral 52

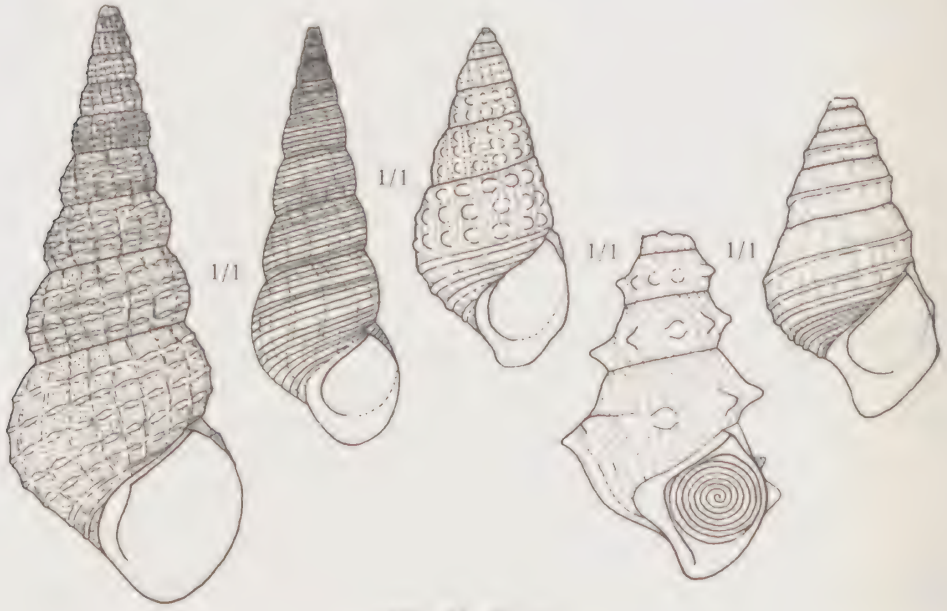


FIG. 74. *Brotia.*

52(51) Shell subovately, ovately or subglobosely conic; operculum multispiral (Fig. 75). Fresh water . . . . . Genus *Paracrostoma*

Shell narrowly or elongately conic; operculum paucispiral 53

75

76

FIG. 75. *Paracrostoma.* FIG. 76. *Thiara.*

53(52) Shell surface sculpture includes spines (Fig. 76). Fresh and brackish water . . . . . Genus *Thiara*

Shell smooth or variously sculptured, but without spines 54

54(53) Shell surface with tubercles 55

Shell smooth or with ribs, lirae, or spiral striae and cords, but generally without tubercles 56

55(54) Shell narrowly conical; whorls without shoulders (Fig. 77). Fresh and brackish water . . . . . Genus *Melanoides*

Shell elongately conical; whorls shouldered (Fig. 78). Fresh and brackish water . . . . . Genus *Tarebia*

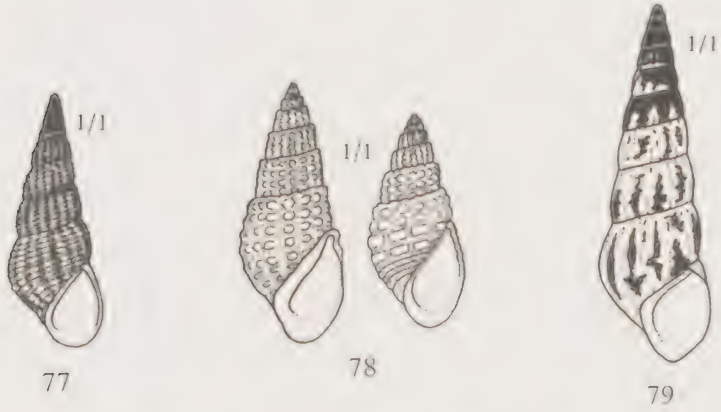


FIG. 77. *Melanoides*. FIG. 78. *Tarebia*. FIG. 79. *Adamietta*.

56(54) Shell smooth (Fig. 79). Fresh water . . . . . Genus *Adamietta*

Shell sculptured with spiral grooves and transverse ribs 57

57(56) Shell with spiral grooves only, no transverse sculpture (Fig. 80). Fresh water . . . . . Genus *Neoradina*

Shell with spiral grooves or ridges, and with transverse ribs 58

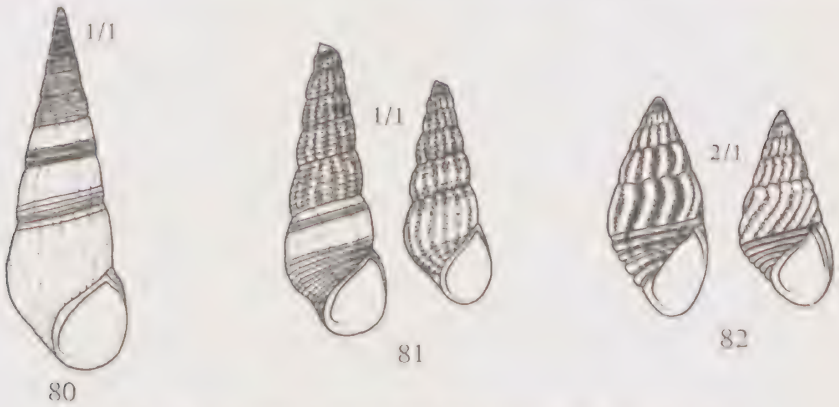


FIG. 80. *Neoradina.* FIG. 81. *Melanoides.* FIG. 82. *Sermyla.*

58(57) Shell narrowly conical, sculptured with spiral grooves and weak or strong transverse ribs (Fig. 81). Fresh and brackish water . . . . Genus *Melanoides*

Shell elongately conical, sculptured with strong transverse ribs, and with strong spiral ridges on the shell "base", but without spiral grooves (Fig. 82). Brackish water . . . . . Genus *Sermyla*

59(1) Shells generally rather thick and solid, with lamellae or "teeth" in the aperture or on the columella. Brackish water and land. Order Actinophila. Family Auriculidae 60

Shells rather thin, without lamellae or "teeth" in the aperture or on the columella. Fresh water 66

60(59) Shell large, 30 mm or more in length (Fig. 83). Brackish water . . . Genus *Ellobium*

Shell medium or small, less than 30 mm in length 61

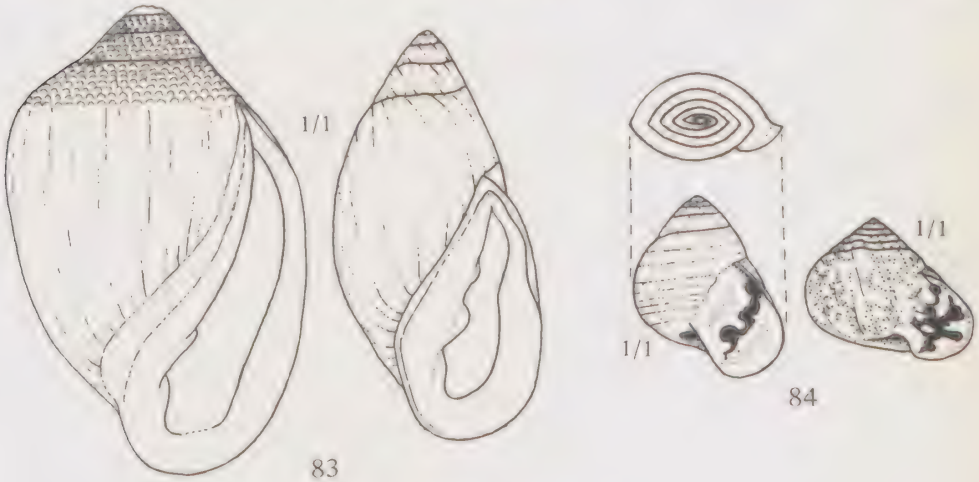


FIG. 83. *Ellobium.* FIG. 84. *Pythia.*

61(60) Shell dorsoventrally flattened (Fig. 84). Brackish water . . . . . Genus *Pythia*

Shell round in end view, not dorsoventrally flattened 62

62(61) Outer lip flattened dorsoventrally, bordered on the inside by a thick sharp ridge, and on the outside by a thick varix (Fig. 85). Brackish water . . . . . Genus *Cassidula*

Outer lip not flattened dorsoventrally, not bordered on the inside by a ridge or on the outside by a varix 63

FIG. 85. *Cassidula.* FIG. 86. *Cylindrotis.*

63(62) Shell small, cylindrical (Fig. 86). Brackish water . . . . . Genus *Cylindrotis*

Shell medium to small, spindle-shaped 64

64(63) Shell narrowly spindle-shaped; aperture without palatal lamellae or teeth (Fig. 87). Brackish water . . . . . Genus *Auriculastra*

Shell broadly spindle-shaped, aperture with palatal lamellae or teeth 65

FIG. 87. *Auriculastra.* FIG. 88. *Laemodonta.* FIG. 89. *Melampus.*

65(64) Shell small, surface with strong spiral sculpture of grooves or pits (Fig. 88). Brackish water . . . . . Genus *Laemodonta*

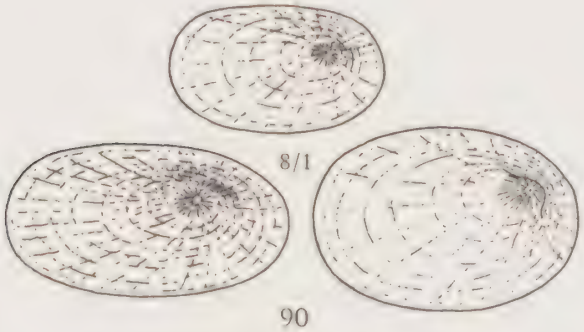
Shell medium to small, surface smooth, or with only weak spiral sculpture (Fig. 89). Brackish water . . . . . Genus *Melampus*

66(59) Shell cap-like (limpet-shaped; ancyliform), not coiled. Superfamily Ancyloidea, in part: Family Ancylidae 67

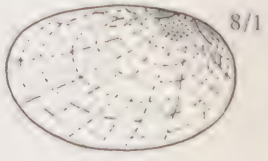
Shell coiled, not cap-like 68

67(66) Shell apex sculptured with radiating striae; apex submedianly placed (Fig. 90). Fresh water . . . . . Genus *Pettancylus*

Shell apex sculptured with irregular pits; apex near right shell margin (Fig. 91). Fresh water . . . . . Genus *Gundlachia*[14]



90



91

FIG. 90. *Pettancylus.* FIG. 91. *Gundlachia.*

68(66) Shell planate or planorboid (planispiral; discoidal), coiled in one plane (Fig. 92). Superfamily Ancyloidea, in part: Family Planorbidae, in part 69

Shell elongate, not planate 72

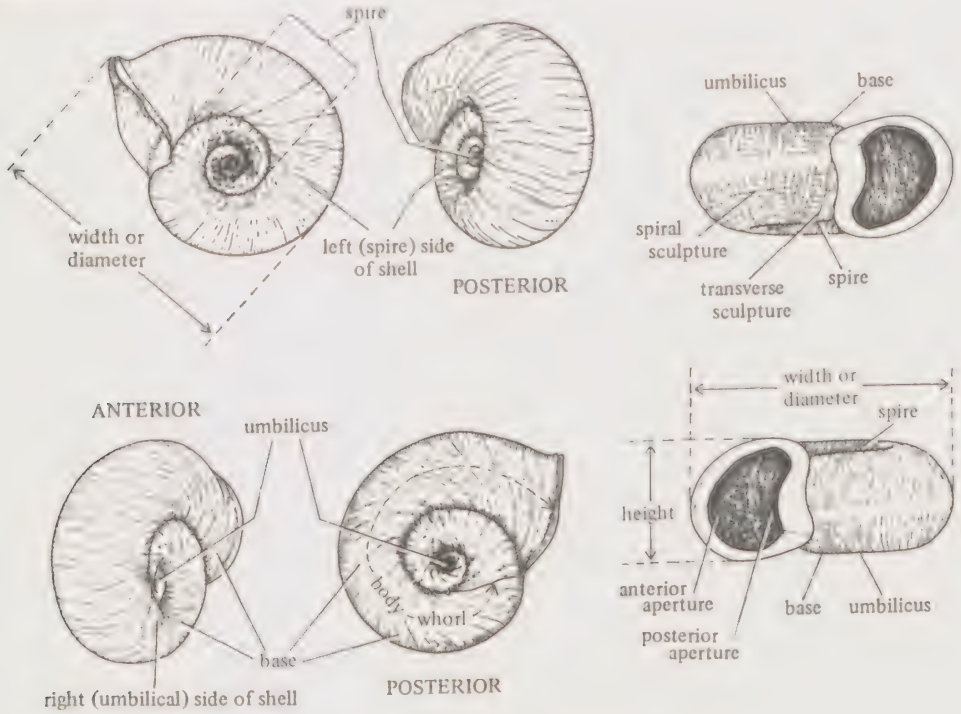


FIG. 92. Terminology of a planorboid shell.

69(68) Adult shell of medium size, more than 1 cm in diameter (Fig. 93). Subfamily Bulininae. Fresh water . . . . . Genus *Indoplanorbis*

Adult shell small, less than 1 cm in diameter. Subfamily Planorbinae 70

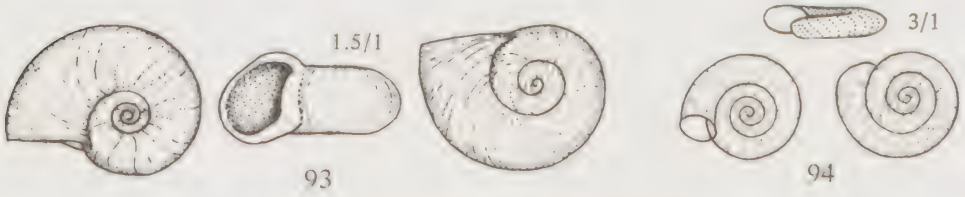


FIG. 93. *Indoplanorbis.* FIG. 94. *Gyraulus.*

70(69) Inverted spire wide and shallow; basal or umbilical side of shell flattened (Fig. 94). Fresh water . . . . . Genus *Gyraulus*

Inverted spire relatively narrow and deep; basal or umbilical side of shell convexly curved 71

71(70) Shell with periodic internal lamellae in the last whorl (Fig. 95). Fresh water . . . . . Genus *Polyphylis*[15]

Shell without internal lamellae (Fig. 96). Fresh water . . . . . Genus *Helicorbis*

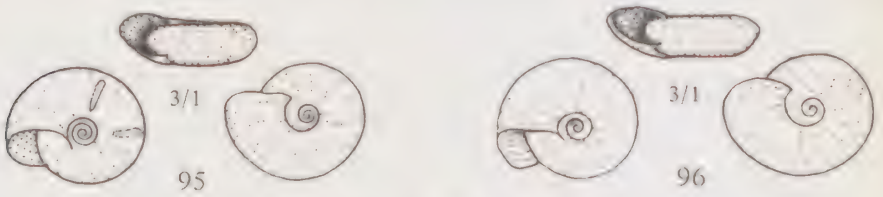


FIG. 95. *Polyphylis.* FIG. 96. *Helicorbis.*

72(68) Shell coiled to the left (sinistral) (Fig. 97). Superfamily Ancyloidea, in part: Family Planorbidae, in part 73

Shell coiled to the right (dextral) (Fig. 98). Superfamily Lymnaeoidea, Family Lymnaeidae[16] 74

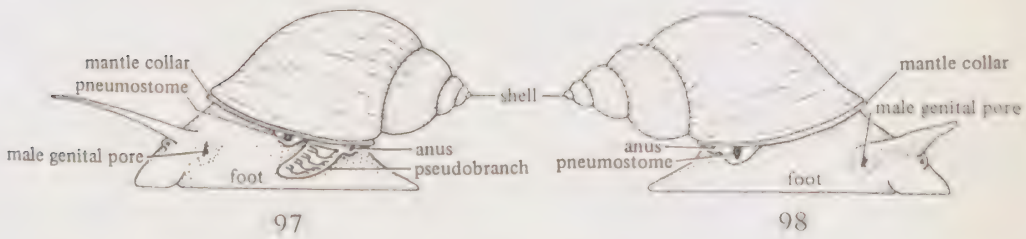


FIG. 97. Sinistral shell and animal. The shell is coiled to the *left* and the respiratory, excretory and reproductive openings are on the *left* side. FIG. 98. Dextral shell and animal. The shell is coiled to the *right* and the respiratory, excretory and reproductive openings are on the *right* side.

73(72) Whorls rounded, without shoulders (Fig. 99). Fresh water . . . . Genus *Camptoceras*

Whorls angularly shouldered (Fig. 100). Fresh water . . . . . Genus *Amerianna*[14]

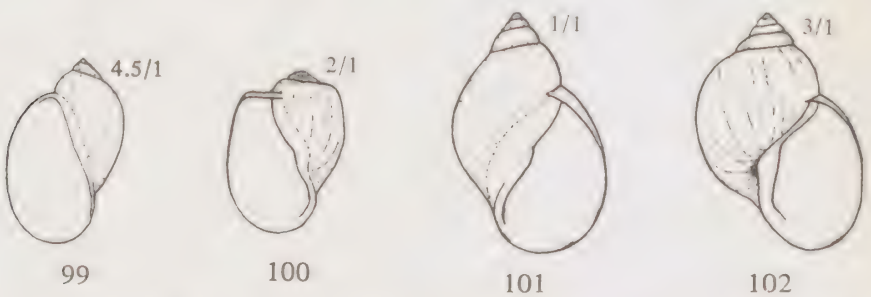


FIG. 99. *Camptoceras.* FIG. 100. *Amerianna.* FIG. 101. *Radix.* FIG. 102. *Austropeplea.*

74(72) Adult shell larger, 15 mm or more in length; columella generally twisted, making a fold or plait at the apertural margin (Fig. 101). Fresh water . . . . . Genus *Radix*

Adult shell smaller, less than 15 mm in length; columella generally straight, without a fold or plait at the apertural margin (Fig. 102). Fresh water . . . . . Genus *Austropeplea*

NOTES

[1] This key was prepared by the junior author, with the assistance of Drs. Upatham, Sornmani, Kitikoon and Lohachit, as part of the development of a research and training program on medically important and other mollusks of Southeast Asia. We wish to acknowledge the aid of Mrs. Pusadee Sri-Aroon (nee Butrcham) and Mrs. Nauwarath Sukhapanth.

In a dichotomous "key" such as the one presented here, the reader with a snail to identify is presented with a successive series of two opposing choices ("couplets") about one or more characters (usually morphological) possessed by the animal whose identity is to be determined. In each successive couplet of the key, only one of the opposing sets of characters should fit the specimen in question, the choice of which leads the reader to the next couplet of opposing choices. This procedure is followed until a couplet leads the reader to a taxon name (in this key, to a genus) rather than the number of another couplet. This taxon name identifies the animal in question.

[2] Among the Thai Prosobranchia, *Rivomarginella morrisoni* Brandt (Neogastropoda, Marginellidae) is an exception in that it lacks an operculum. Otherwise, *R. morrisoni* has all the typical prosobranch characteristics.

[3] Higher taxonomic categories (subclass, order, superfamily, family, subfamily, tribe) are given at the appropriate places in the key. However, the couplet characters are for the purpose of identifying only the Thai fresh- and brackish-water snails, and therefore the characters used in the couplets are not necessarily diagnostic for the higher taxonomic categories on a world-wide basis.

[4] The great majority of the Opisthobranchia lack an operculum, but the Pyramidellidae are one of the primitive opisthobranch groups that have retained this structure.

[5] Brandt (1974, *Arch. Molluskenkd.*, 105: 207) indicated that some protoconchs in *Morrisonietta* are "homoeostrophic".

[6] Neritidae auct. is a synonym of Neritinidae Rafinesque 1815 but, since the latter is a *nomen oblitum*, it seems best to use the better known name Neritidae.

[7] The ending *-oidea* for superfamilies is recommended by the International Commission on Zoological Nomenclature instead of *-acea*, which is commonly used in malacological literature.

[8] The opercula of the Iravadiidae (Fig. 48a) and the Stenothyridae (Fig. 55b) have ridges on their inner surfaces.

[9] *Wattebledia baschi* Brandt (Mesogastropoda, Bithyniidae) is an exception, having a notch in the anterior apertural margin.

[10] Generic assignments in the Thai Viviparidae are based largely on adult shell characters, a practice which is not altogether satisfactory. The family needs much further study.

[11] *Mekongia jullieni* (Deshayes) [extralimital, but type species of the genus] is reported (Brandt, 1974, *Arch. Molluskenkd.*, 105: 39) to have an obtuse carina around the embryonic shell periphery, making it an exception among the smooth-shelled embryos of *Mekongia.*

[12] The identification key to the Assimineidae is from Brandt (1974, *Arch. Molluskenkd.*, 105: 141).

[13] "Shells [of *Karelainia*] virtually indistinguishable from those of *Paraprososthenia*". The two genera are distinguished on anatomical characters: "*Karelainia* differs from all other triculine genera by bursa copulatrix nearly fusing to oviduct, by narrow diameter of oviduct circle complex with bursa posterior to coil" (Davis, 1979, *Monogr. Acad. nat. Sci. Phila.*, 20: 111).

[14] Artificially introduced by man in recent times.

[15] Lamellae occur on the inner shell surface in the body whorl of *Polyphylis*, but not within the aperture itself.

[16] In many reports, all lymnaeids in Southeast Asia are included in the Holarctic genus *Lymnaea*. However, the southern and southeastern Asian and Australasian lymnaeids belong to a different stock from the Holarctic *Lymnaea stagnalis*, the type species of the genus *Lymnaea*. Two species groups (genera or subgenera) of Lymnaeidae occur in Thailand, *Radix* and *Austropeplea.*

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MINA L. WINSLOW
1890-1982

Mina L. Winslow was the first curator of mollusks at the Museum of Zoology, The University of Michigan. She was appointed to that position in 1914, after receiving her Masters Degree from The University of Michigan, and remained until her retirement in 1929. During her 15 years of service, Miss Winslow organized and managed the University's acquisitions of mollusks and added substantially to the Museum's holdings. Previous to Miss Winslow's appointment as Curator, the Museum's accumulation of mollusks was simply part of a general collection of zoological specimens.

Miss Winslow was born in Chicago, Illinois. She graduated from Smith College, Northampton, Massachusetts, in 1913, and enrolled that same year in The University of Michigan as a graduate student in zoology.

One of the highlights of Miss Winslow's career as a malacologist was a collecting trip in 1924 to southern Africa. She was away from the University for a year, leaving Ann Arbor in April 1924 and returning in March 1925. During this trip, she collected not only mollusks, but insects and herpetological specimens as well. A more detailed account of this trip will be published in *Walkerana*. In 1969, at the age of 79, Miss Winslow returned to southern Africa, revisiting many of the localities of her first trip.

During her many years of retirement, Miss Winslow continued to live in Ann Arbor, but spent the winters in Mexico. She travelled extensively, not only to Mexico, but also to Guatemala and Peru, and frequently to Europe. In 1954, she took a trip around the world. Miss Winslow was an accomplished and well-known artist, and for many years she was a member of the Ann Arbor Art Association and the Detroit Society of Women Painters and Sculptors.

circa 1924

1968

Bibliography of Mina Winslow's Publications on Mollusks

An annotated list of shells from northern Michigan. *Occas. Pap. Mus. Zool. Univ. Mich.*, (42): 1-16, 1917.

Pleurobema clava (Lam.) and *Planorbis dilatatus buchanensis* (Lea) in Michigan. *Occas. Pap. Mus. Zool. Univ. Mich.*, (51): 1-6, pl. 1, 1918.

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Mollusca from North Dakota. *Occas. Pap. Mus. Zool. Univ. Mich.*, (98): 1-18, 1921.

Shells from Alcona, Oscoda and Crawford counties, Michigan. *Occas. Pap. Mus. Zool. Univ. Mich.*, (102): 1-5, 1921.

Notes on the internal lamellae of *Carychium*. *Occas. Pap. Mus. Zool. Univ. Mich.*, (128): 1-7, pls. 1-5, 1922.

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The varieties of *Planorbis campanulatus* Say. *Occas. Pap. Mus. Zool. Univ. Mich.*, (180): 1-9, pls. 1, 2, 1926.

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List of Mollusks Described by Mina Winslow with Their Original References, Type Localities and Museum Catalogue Numbers

davisi Winslow, ***Planorbis campanulatus*** [*Planorbella*]: 1926, *Occas. Pap. Mus. Zool. Univ. Mich.*, (180): 8, pl. 2, figs. 17-19. Pinnebog River, Huron County, Michigan. Holotype UMMZ 83451 [Bryant Walker coll. no. 9974]; paratypes UMMZ 35808, 83452.

jordanensis Winslow, ***Planorbis antrosus*** [*Helisoma anceps*]: 1923, *Occas. Pap. Mus. Zool. Univ. Mich.*, (145): 1, pl. 1, figs. 1-5. South arm of Pine Lake, about two miles north of East Jordan, Charlevoix County, Michigan. Holotype UMMZ 27440; paratypes UMMZ 82428, 27444, 29953.

michiganensis Winslow, ***Ferrissia***: 1923, *Occas. Pap. Mus. Zool. Univ. Mich.*, (145): 2, pl. 1, figs. 6-8. Willow Brook west of Harbert, Chickaming Township, Berrien County, Michigan. Holotype UMMZ 13057; paratypes UMMZ 13058, 13059, 100551.

wisconsinensis Winslow, ***Planorbis campanulatus*** [*Planorbella*]: 1926, *Occas. Pap. Mus. Zool. Univ. Mich.*, (180): 5, pl. 2, figs. 14-16. Little Arbor Vitae Lake, Vilas County, Wisconsin. Holotype UMMZ 35890; paratypes UMMZ 35793.

Subspecies Named after Mina Winslow

winslowi F.C. Baker, *Planorbis trivolvis* [*Planorbella*]: 1926, *Nautilus*, 39(4): 116. Little Arbor Vitae Lake, Vilas County, Wisconsin. Holotype UMMZ 35803; paratypes UMMZ 35804.

J.B. BURCH

NEWS AND ANNOUNCEMENTS

* * * * *

UNITAS MALACOLOGICA. - *Unitas Malacologica* is an international organization of malacologists and malacological societies whose goal is to support malacological research throughout the world and to regularly organize international malacological Congresses. The originally European society, founded in 1962 in London, was changed into a more broadly international organization in 1977 and now has more than 200 members all over the world. Its legal domicile is Basle, Switzerland. The annual subscription is 20 Swiss francs. This membership fee includes the Proceedings of the Congresses, held every third year. The last Congress was held in Perpignan, France, in 1980. The next International Malacological Congress will be held in Budapest, Hungary, in 1983.

Questions and applications with respect to membership should be sent to the Secretary, Dr. Oliver E. Paget, Natural History Museum, Burgring 7, A-1014 Vienna, Austria.

SOCIEDAD ESPAÑOLA DE MALACOLOGÍA. – The Sociedad Española de Malacología, with its head office in Madrid, was established in August, 1980, its purpose being the promotion and diffusion of malacological studies by means of conventions and publications. This society, of national scope, is also open to scientists and any others in foreign countries who are interested in malacology.

The scientific publication of the Sociedad is *Iberus* (see p. 152 of this issue of *Malacological Review*).

The members of the Executive Staff are: *President*, Julio Alvarez Sánchez; *Vice-president*, Jordi Martinell Callicó; *Secretary*, Angel A. Luque del Villar; *Treasurer*, José Templado González; *Librarian*, Roberto Llansó Martín-Moreno; *Publications editor*, Fernando Pereira Ramos; *Executive members*, Yolanda Manga González, Miguel Ibáñez Genis, Joandomenec Ros i Aragonés, Miguel De Renzi de la Fuente, Antonio Figueras Montfort and Pedro Antonio Talavera Torralba.

The head office of the Sociedad Española de Malacología is in the Museo Nacional de Ciencias Naturales, Paseo de la Castellana, 80, Madrid-6, Spain.

MALACOLOGICAL SOCIETY OF THE PHILIPPINES. – The Malacological Society of the Philippines was founded in 1980. The aims of the Society are to generate greater interest in the formulation of researches in malacology; to establish a good museum collection of medically important freshwater and land snails; and to hold regular annual meetings and seminars on recent advances in the field of malacology.

The officers of the society are as follows: *President*, Ruben Umaly, Department of Zoology, University of the Philippines; *Vice-president*, Nonette Jueco, Institute of Public Health, University of the Philippines; *Secretary*, Edith Alikpala, Department of Zoology, University of the Philippines; *Treasurer*, Marisa Ramos, Natural Science Research Center; *Regional officers* (for Luzon, Visayas and Mindanao), Merle Macaranag, Eraklio Banez, Rebecca Rayo, Ray Rose Libed, Jonathan Placido and Roger Pangilinan. Dr. B.C. Dazo, World Health Organization, Manila, and Dr. J.B. Burch, The University of Michigan, are Advisors.

The newly accepted members are: Merle Macaranag, Ruth Martinez, Erlinda Sarmiento and Eduardo Varona (Schistosomiasis Control and Research Service, Manila); Eraklio Banez, Daisy Perez, Maximino Villordon, Melba Pineda, Betty de la Calzada, Teresita Maula (Schistosomiasis Control and Research Service, Palo, Leyte); Jesusa Louh and Jonathan Placido (Schistosomiasis Control Team, Tagum, Davao del Norte); Nelson Mendez (Schistosomiasis Control Team, San Francisco, Agusan del Sur); Jose Feliciano and Aurora Vergel (Schistosomiasis Control Team, Cabadbaran, Agusan del Norte); Olivia Vicente (Schistosomiasis Control Team, Borongan, Samar); Ray Rose Libed (Schistosomiasis Control Team, Alegria, Surigao del Sur); Rosalina Pacheco (Schistosomiasis Control Team, Trinidad, Bohol); Modesto Pacleb, Jr. (Schistosomiasis Control Team, Isulan, Sultan Kudarat); Rebecca Rayo and Patria Kintana (Schistosomiasis Control Team, Dipolog, Zamboanga del Norte); Emerita Daluz (Schistosomiasis Control Team, Kapatagan, Lanao del Norte); Imelda Rosales, Veronica Clarin, Imelda Fornillos, Manuel Nivera and Evelyn Bolante (NISIP I, Palo, Leyte); Dario Bibere (NISIP II, Victoria, Oriental Mindoro); Daisy Berdon and Henry Montes (NISIP II, Molave, Zamboanga del Sur); Rogelio Pangilinan and Florante Rante (NISIP II, M'lang, North Cotabato); Antonio Casuga (NISIP II, Digos, Davao del Norte); Florida Octavo (Mindoro Irrigation Development Project, Victoria, Oriental Mindoro); Poncelo Cac (Samar Irrigation Development Project, Catbalogan West Samar); Manuel Collado (Bukidnon Irrigation Development Project, Malaybalay, Bukidnon); Elpidio Remigio and Roberto Pagulayan (Natural Science and Research Center, University of the Philippines); and Flora Caro (Institute of Public Health, University of the Philippines).

FRESHWATER MALACOLOGY RESEARCH GROUP ESTABLISHED AT THE UNIVERSITY OF THE PHILIPPINES, QUEZON CITY, PHILIPPINES. – After a series of meetings in August 1981, a group of faculty members of the Department of Zoology of the College of Arts and Sciences, University of the Philippines, organized a research team aimed at working on selected aspects of the biology of freshwater gastropods of medical and economic importance. The objectives of the malacology research program are to: (1) obtain some basic information on certain biological aspects (taxonomy, morphology, physiology, reproductive and developmental biology, genetics, ecology and distribution) of selected freshwater gastropods; (2) establish a freshwater snail reference collection for the Philippines; (3) use information obtained for a more logical malacological program in the control of snail-mediated parasitic infections; (4) use information obtained for possible commercial-scale culturing of economically important snails; and (5) develop malacology as an area of specialization of the Department of Zoology, University of the Philippines.

Among the projects proposed by the various researchers are: (1) Geographical strains, ecology and population dynamics of *Oncomelania hupensis quadrasi*, the intermediate host of *Schistosoma japonicum*, in the Philippines – Ruben C. Umaly, Ph.D.; (2) Growth and development of *Pila luzonica* and *Melania* spp. – Jermelina Garibay, B.S., and Ma. Edith Hermosura, B.S.; (3) Characteristics of the hemolymph antigens of selected snails of medical importance – Ronald Matias, B.S.; (4) The effects of gamma irradiation on the hemolymph cells of various lymnaeids and *Oncomelania hupensis quadrasi* – Ruben C. Umaly, Ph.D., and Corazon Cuaresma, B.S.; (5) Studies on hormonal control of reproduction in *Pila luzonica* – Ruth Dotimas, B.S.; (6) The systematic relationship of *Lymnaea (Radix) swinhoie* var. *quadrasi* von Moellendorf and *Lymnaea viridis* Quoy and Gaimard – Imelda Pagulayan, M.S.; (7) Taxonomy and distribution of freshwater snails of the Philippines with notes on their ecology – Edith Alikpala, M.S., Ang Put, Jr., B.S., Ma. Lourdes Cuvin, B.S., and Luis Lagera, Jr., B.S.

The program is headed by Dr. Ruben C. Umaly, and the group has Dr. Bonifacio Dazo of the World Health Organization (Manila) and Dr. J.B. Burch of The University of Michigan (Ann Arbor) as technical advisors.

SOUTHEAST ASIAN CENTER FOR APPLIED MALACOLOGY ESTABLISHED AT MAHIDOL UNIVERSITY, BANGKOK, THAILAND. – The Center for Applied Malacology in Southeast Asia was established in late 1978 at Mahidol University with an Institution Strengthening Grant from the World Health Organization Special Programme for Research and Training in Tropical Diseases. The long-term objectives of the Center are to: (1) undertake research and training programmes of particular relevance to the region; (2) function as a reference laboratory for snail-host identification and advisory services, as well as maintenance of living and preserved mollusk/parasite stock materials; (3) collaborate closely with and assist in the coordination of other laboratory and field programmes on applied malacology.

The subsidiary long-term objectives of the Center include: (1) the development and standardization of methods, terminology, diagnostic procedures, and field control strategy; (2) the distribution, upon request, of preserved specimens of standard snail-host/parasite strains; (3) the development of training programmes at both professional and sub-professional levels; (4) the preparation, publication and dissemination of information, e.g., scientific journals, manuals, brochures, etc.; (5) the provision of consultant assistance as required.

The Center for Applied Malacology has established an administrative structure and procedures for the operation of the multi-laboratory center; partly trained and up-graded national staff; initiated a reference collection of local snails of medical and socio-economic importance; developed culture methods for the schistosome-bearing snails; and developed a practical and safe snail disposal procedure and containment.

MASTER OF SCIENCE COURSE IN ENVIRONMENTAL SCIENCE AND DEVELOPMENT AT THE UNIVERSITY OF SUSSEX, ENGLAND, U.K. – This course is intended to provide a new structure for evaluating some of the major, man-made, medical, veterinary and agricultural problems facing the people of both the developing and developed world today. These include schistosomiasis, fascioliasis, malaria, salination resulting from irrigation and the control of pests of agricultural crops, as well as general problems associated with technological development. Previous attempts at providing solutions have often failed because the approach was simplistic, involving specialists working in isolation within a narrow discipline. The present approach will be interdisciplinary, involving scientists from the Schools of Biological Sciences, Chemistry and Molecular Sciences, and Mathematical and Physical Sciences, the ARC Unit of Insect Chemistry and Physiology, the Science Policy Research Unit, and the Institute of Development Studies.

Applications must be made on an official application form not later than July 1st (for the course starting in October of the same year) and successful candidates usually will be informed by the end of the month. Application forms and a prospectus providing further information can be obtained from: The Subject Chairman, Biology Subject Group, School of Biological Sciences, University of Sussex, Falmer, Brighton BN1 9QG, East Sussex, England.

MALACOLOGY AT THE UNIVERSITY OF MICHIGAN. – The University of Michigan has long been one of the major training centers for malacologists, especially for those dealing with freshwater and land mollusks. Over the years, some forty students specializing in some aspect of malacology have received Ph.D. degrees from the University. B.Sc. and M.Sc. degrees also have been awarded. Students in malacology have specialized in such diverse areas as taxonomy, zoogeography, ecology, comparative and functional morphology, developmental biology, reproductive physiology, carbohydrate biochemistry, genetics, cytogenetics/cytotaxonomy, medical malacology/parasitology and paleontology. The program at The University of Michigan is a flexible one, designed to give the student a basic background in malacology, exposure to many aspects of the biology of mollusks, and, at the Ph.D. level, to give the student highly specialized training for basic research on mollusks. High academic standards are emphasized. Training leading to B.Sc., M.Sc. and Ph.D. degrees may be pursued either in the College of Literature, Science, and the Arts, the School of Natural Resources, or the School of Public Health. Collaborative training programs exist with other institutions in the United States and in Thailand, Philippines, Korea, Jordan, Egypt, Ethiopia, India and Cuba. Further information may be obtained by addressing inquiries to the Mollusk Division, Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109, U.S.A.

NEW NAME AND POLICIES OF THE *BULLETIN OF THE AMERICAN MALACOLOGICAL UNION*. – At the last meeting of the American Malacological Union, the name of the society's annual publication, recently known as the *Bulletin of the American Malacological Union*, was changed to the *American Malacological Bulletin*. In addition to its new name, the *Bulletin* is taking on a new format, a new editor, new printer and a new editorial policy. A permanent Board of Editors and Board of Reviewers have been compiled from some of the world's most prominent malacologists. The newly revamped *Bulletin* is now accepting qualified manuscripts for publication. Manuscripts of any length dealing with any aspect of molluscan research will be reviewed by at least two internationally acknowledged malacologists with pertinent expertise. Papers should basically follow the style outlined in the *Council of Biology Editors Style Manual*, 4th ed., 1978, American Institute of Biological Sciences, 1401 Wilson Blvd., Arlington, Virginia 22209, U.S.A. The papers need *not* have been presented at the annual American Malacological Union meeting. Thus, a new outlet for high quality research papers dealing with marine, freshwater or terrestrial molluscs will appear with Volume 1, Number 1, in early 1983. For more information concerning preparation of manuscripts or subscriptions, please contact Dr. Robert S. Prezant, Editor, *American Malacological Bulletin*, Department of Biology, University of Southern Mississippi, Hattiesburg, Mississippi 39406, U.S.A.

SECOND INTERNATIONAL WORKSHOP ON THE MALACOFAUNA OF HONG KONG AND SOUTHERN CHINA. – Between 6 and 24 April 1983, the University of Hong Kong is organizing a second research workshop on the molluscan fauna of Hong Kong and its coastal seas. The workshop will be convened at residential laboratories in Wu Kwai Sha, the New Territories of Hong Kong. Boat, diving and car collecting facilities will be made available to participants, as well as laboratories, aquaria and equipment. There is no registration fee and costs of accommodation and board (breakfast, packed lunch and dinner) will be approximately US$20/day. Participants will undertake research either on their own or in cooperation with local scientists upon any chosen aspect of the region's rich terrestrial, fresh water or marine Mollusca. A programme of evening seminars will be held. The last three days of the workshop will be in the city where a programme of tours and visits can be arranged. For these three days, participants are expected to organize their own hotel accommodations. Interested potential participants should write to Professor Brian Morton, Department of Zoology, The University, Hong Kong.

The Proceedings of two previous workshops are available from the publisher: Hong Kong University Press, Hong Kong. (*Proceedings of the first international workshop on the malacofauna of Hong Kong and southern China*, 1980, 345 pp., HK$60 (US$10); *Proceedings of the first international marine biological workshop: the marine flora and fauna of Hong Kong and southern China*, 1982, 2 vols., 933 pp., HK$228.50 (US$38)).

THE SECOND INTERNATIONAL *CORBICULA* SYMPOSIUM. – The Second International *Corbicula* Symposium will be held in Hot Springs, Arkansas, U.S.A., 21-24 June 1983, to examine and assess basic and applied studies related to the problem of *Corbicula* biofouling and control, to explore further some aspects of the basic biology of the organism, and to summarize the investigative findings and search for consensus, conclusions and practical applications among them. The Steering Committee is committed to the concept that this meeting should open dialogue between industrial personnel and biologists, so that their efforts can be more effectively focused toward understanding biofouling problems and devising effective measures of control. For additional information, write to Dr. Joseph C. Britton, Department of Biology, Texas Christian University, Fort Worth, Texas 76129, U.S.A.

THE EIGHTH INTERNATIONAL MALACOLOGICAL CONGRESS, sponsored by the *Unitas Malacologica*, will be held in Budapest, Hungary, from 29 August to 3 September 1983. Further information can be obtained by writing to Dr. László Pintér, *Unitas Malacologica*, c/o Natural History Museum, Baross u. 13, H-1088 Budapest, Hungary.

FIFTH CONGRESS OF THE SOCIÉTÉ FRANÇAISE DE MALACOLOGIE AND THE ITALIAN-FRENCH-SPANISH SYMPOSIUM ON MEDITERRANEAN SHELL-CULTURE. – The Fifth Congress of the Société Française de Malacologie will be held at Ile des Embiez (Var), France, on 5-10 September 1983. An Italo-Franco-Spanish Symposium on "Conchyliculture Mediterranéenne" will be held in conjunction with the Congress. For further information, write to Fondation Oceanographique Ricard, Ile de Embiez, 83140 Six-Fours, France.

SOCIETÁ ITALIANA DI MALACOLOGIA. – Beginning in 1983, the Società Italiana and the Unione Malacológica Italiana will unite to form the Società Italiana di Malacologia. The new society will include all the members of the two former societies. For further information, correspondence may be directed to the Museo Civico di Storia Naturale, Corso Venezia, 55, 20121 Milano, Italy.

NORTH AMERICAN FRESHWATER SNAILS. – Two parts of a three-part series on *North American Freshwater Snails* have now been published:

Species List, Ranges and Illustrations, by J.B. Burch & John L. Tottenham, 135 pp., 751 figs., 1980
Identification Keys, Generic Synonymy, Supplemental Notes, Glossary, References and Index, by J.B. Burch, 149 pp., 280 figs., 1982.

These two parts can be ordered from *Malacological Review*, P. O. Box 637, Niwot, Colorado 80544, U.S.A. Their prices are US$20.00 and $25.00, respectively, postpaid.

MALACOLOGICAL REVIEW, SUPPLEMENTS 1 AND 2. – Supplements 1 and 2 are available from *Malacological Review* at the prices given below. They can be ordered from *Malacological Review*, P. O. Box 637, Niwot, Colorado 80544, U.S.A.

Supplement 1. *Freshwater snails of Taiwan (Formosa)*, by Gary L. Pace. This illustrated monographic study deals with the identification, classification, distribution, zoogeographic affinities and parasitological importance of thirty-nine species of Formosan freshwater gastropod mollusks. US$15.00, postpaid.

Supplement 2. *The Mekong schistosome*, J.I. Bruce, S. Sornmani, H.L. Asch & K.A. Crawford, Editors. This publication is a monograph on the newly discovered human blood fluke, *Schistosoma mekongi*, and its unusual molluscan host, *Tricula aperta*. In addition to details on the parasite, this book presents various studies on the snail intermediate host, including its anatomy, systematic and zoogeographic relationships, evolution, habitats and bionomics, laboratory maintenance and culture, susceptibility to the parasite, effect of the parasite on the snail, the snails' role in disease transmission, and sensitivity of the snails to molluscicides. US$26.00, postpaid.

MALACOLOGICAL REVIEW, SUPPLEMENT 3. – Supplement 3, *A dissection guide, field and laboratory manual for the introduced bivalve* Corbicula fluminea, by Joseph C. Britton & Brian Morton, is now available. In 1944, the Asian clam *Corbicula fluminea* was discovered in a wild uninhabited section of the Columbia River in Washington State, U.S.A. Since then, the clam has spread rapidly down the West Coast and across the southern United States to Florida, and northward into the Mississippi and other river systems. In many places, *Corbicula* has become a very serious pest, invading commercial gravel beds, clogging water mains, fouling filtration plants, etc. Also, it probably is having a detrimental effect on the native North American fauna, already threatened by water pollution, habitat destruction and human exploitation. *Corbicula* can reproduce more rapidly, grow faster and is more adaptable than most native North American species.

Britton & Morton's manual is a timely publication on *Corbicula* in North America. It documents the clam's past history and spread on this continent, and deals with its taxonomy, nomenclature, ecology, functional morphology and physiology. Various laboratory exercises are presented whereby these numerous and common clams can be used to demonstrate aspects of molluscan bivalve biology.

To order, send US$16.00 per copy (includes postage and handling) to: *Malacological Review*, P. O. Box 637, Niwot, Colorado 80544, U.S.A.

SIXTH MEETING ON THE INVESTIGATION OF MOLLUSCS, U.S.S.R. – The Sixth Meeting on the Investigation of Molluscs took place in Leningrad on 7-9 February 1979. Titles of the papers presented at the Meeting are given below. Those marked with an asterisk have English language abstracts in addition to the Russian abstracts. For further information, contact Prof. I.M. Likharev, Zoological Institute, U.S.S.R. Academy of Sciences, Leningrad V-164, U.S.S.R.

PROGRAM

*Agarova, I.I. Some aspects of the linear growth of bivalve molluscs in a population of *Cerastoderma edule belgicum*.

*Akramowski, N.N. The history of formation of the land and freshwater molluscan fauna in the eastern part of the Transcaucasian upland.

*Alexandrov, D.A. & Sergievsky, S.O. A variant of sympatric speciation in snails.

Alimov, A.F. Functional-ecological features of freshwater bivalve populations.

*Almuhambetowa, S. Pupilloidea of the Talass Alatau Mountains.

*Alyakrinskaya, I.O. Adaptations of mollusc embryos to nutrition and respiration.

*Amitrov, O.V. The marine Paleogene gastropods from southern USSR (comparative analysis of assemblages).

Antipova, T.V. Zoogeographical characteristics of the Bivalvia of the Barents Sea and the Kara Sea.

*Antonov, P.I. The possibility of age determination in *Dreissena polymorpha* (Pallas) by the structure of the septal surface.

Arakelova, E.S. The influence of reduced oxygen content on the metabolic rate of prosobranch snails.

Arsan, O.M. Dependency of the activity of respiratory enzymes in the tissues of bivalve molluscs on phosphorus content.

Babak, E.V. The history of the family Dreissenidae in the Pliocene-Quaternary Euxinic basin.

*Barskov, I.S. Life-forms and ecogenesis of cephalopods in the Paleozoic.

Beer, S.A. & Lurje, A.A. Radioisotopic marking of freshwater molluscs.

Beljakova, I.V. Freshwater molluscs of Kazakhstan as intermediate hosts of Trematoda.

Berjoskina, G.V., Kiseljova, L.N. & Konstantinova, T.S. Dependence of calcium and magnesium content in the Lymnaeidae shell on species and age of mollusks and on hydrochemical regime of ponds.

Bondarchuk, L.G., Doroshenko, O.V., Stadnychenko, A.P. & Dudko, E.V. On the changes in the vitamin balance in bodies of freshwater gastropod mollusks infected with parthenites of trematodes.

*Bregman, J.E. Morphology and population structure of the bivalve *Patinopecten yessoensis* Jay of the Soviet Far East.

*Bykov, A.N. & Dubinina, I.S. Some peculiarities of larval development of the family Enoploteuthidae in the central-east Atlantic.

Cheremnov, A.D. Results of a study of freshwater molluscs of the Upper Jenisei drainage.

Chernogorenko, M.I. & Kurandina, D.P. Investigations on the digenean trematode fauna of Prosobranchia from the Lower Dniepr collected over a period of several years.

*Chistikov, S.D. Phylogenetic relations of scaphopods.

*Denysenko, S.G. Some aspects of the ecology and growth of the scallop *Chlamys islandica* (Müller) in the Barents Sea.

Dolgin, V.N., Zhernovnikova, G.A. & Novikov, E.A. Freshwater malacofauna of the Irtish drainage area.

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MEETING OF THE SOCIETY FOR EXPERIMENTAL AND DESCRIPTIVE MALACOLOGY. – The 1983 annual business meeting of the Society for Experimental and Descriptive Malacology will be held on 26 February 1983 in Ann Arbor, Michigan, U.S.A.

MALACOLOGY TRAINING COURSE IN JORDAN. – A two-week training course in malacology will be given in April 1983 in Amman, Hashemite Kingdom of Jordan. The course will be sponsored by the Jordanian Ministry of Health, the University of Jordan, and the U.S. Agency for International Development, and will be organized by Drs. M. Rida Tawfiq, Elias K. Saliba, J.B. Burch and John I. Bruce. For further information, contact Dr. Rida, Ministry of Health, P.O. Box 1718, Amman, Jordan.

EIGHTH BRAZILIAN CONGRESS OF MALACOLOGY. – In July 1983, the Eighth Brazilian Congress of Malacology will be held on the campus of the Universidade São Paulo, São Paulo, Brazil. For further information, write to the Sociedade Brasileira de Malacologia, c/o Instituto de Biociências – Depto. Zoologia, Universidade de São Paulo, Caixa Postal 20.520, 01.000 São Paulo, Brazil.

SOUTHEAST ASIAN REGIONAL TRAINING COURSE IN APPLIED MEDICAL AND VETERINARY MALACOLOGY. – An intensive six-week training course in malacology, emphasizing the biology of snail transmitters of human and veterinary diseases, is scheduled to be given in Bangkok at the Southeast Asian Center for Applied Malacology in September and October 1983. The course will be given for nationals of countries of Southeast Asia and the Western Pacific by faculty of Mahidol University, and is being organized by Drs. E.S. Upatham and J.B. Burch (Faculty of Science) and Dr. Viroj Kitikoon (Faculty of Tropical Medicine), Mahidol University, Bangkok 4, Thailand.

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by

Jørgen Knudsen

ON THE PRESENCE OF THE INDO-PACIFIC NUDIBRANCH *HYPSELODORIS INFUCATA* ALONG THE MEDITERRANEAN COAST OF ISRAEL

by

Henk K. Mienis* and Gil Gat**

Basteria

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NATIONAL SHELLFISHERIES ASSOCIATION

Tumwater, Washington

September 5–6, 1980

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PERPIGNAN, FRANCE. 31 August–7 September 1980

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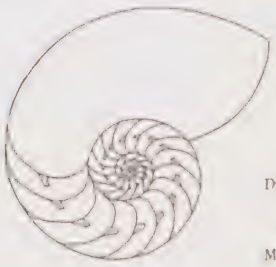

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